SYSTEMATICS OF THE COMMON KINGSNAKE, *LAMPROPELTIS GETULUS* (LINNAEUS) 1

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ABSTRACT

The genus *Lampropeltis* and the species *L. getulus* are defined and relationships are discussed. Individual, ontogenetic, sexual and geographic variation have been analyzed in *L. getulus*. The degree of differentiation among all populations enables the recognition of local populations, microgeographic races, subspecies and subspecies complexes within *L. getulus*. Three subspecies complexes are recognized on the basis of pattern, hemipenial morphology, and intergradation—the *getulus* complex, the *splendida* complex, and the *californiae* complex.

Four subspecies are recognized within the *splendida* complex—*L.g. splendida, L.g. nigritus, L.g. holbrooki,* and *L.g. niger.* Three microgeographic races of *L.g. holbrooki* are distinguished on the basis of pattern. *L.g. splendida* is considered to be closest to the ancestral stock of the species. *L.g. nigritus* is an immediate derivative of *L.g. splendida* by a melanistic reduction in pattern. *L.g. holbrooki* differentiated from the primitive *L.g. splendida* stock by a reduction in the number of dorsal scale rows, and *L.g. niger* evolved from *L.g. holbrooki* by a process of pattern neoteny.

Within the *getulus* complex, two subspecies are recognized—*L.g. getulus* and

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L.g. floridana. A wide zone of intergradation exists in central Florida between the two subspecies as a result of Pleistocene displacement of populations. A disjunct population of *L.g. floridana* occurs in northeastern Florida. The populations in the Apalachicola region of Florida (*L.g. goini*) and the Outer Banks of North Carolina (*L.g. sticticeps*) are considered to be relict intergrades between *L.g. getulus* and *L.g. floridana*. Two microgeographic races of *L.g. getulus* are recognized—a piedmont and a coastal form. *L.g. floridana* is considered a direct derivative of primitive *L.g. splendida* stocks based on similarities of pattern and hemipenial morphology, and the presence of 23 dorsal scale rows. I suggest that ancestral *L.g. floridana* utilized the Gulf Coast Migration Route of the Pleistocene to inhabit the southeastern United States. *L.g. getulus* is derived from *L.g. floridana* by reduction of the number of dorsal scale rows and pattern neoteny.

Only one subspecies within the *californiae* complex is recognized—*L.g. californiae*. The populations exhibiting various banded patterns do not show a significant degree of differentiation worthy of nomenclatural recognition. The striped patterned populations in southern California have been shown to be conspecific with the banded populations (Klauber, 1936, 1939, 1944). Similarly, the striped population in southern Baja California (*L.g. nitida*), on the basis of specimens with a mixed pattern of bands and stripes, has the same relationship with the banded population in southern Baja California (*L.g. conjuncta* = *L.g. californiae*). Specimens intermediate between the striped and banded patterns suggest sympatric intergradation as a result of Pleistocene displacement of populations and all forms are considered as belonging to a single diphyletic subspecies, *L.g. californiae*.

Lampropeltis g. brooksi is considered a synonym of *L.g. floridana*; *L.g. goini* and *L.g. sticticeps* are intergrade populations and are considered synonyms of both *L.g. getulus* and *L.g. floridana*. *L. catalinensis* is shown to be a synonym of *L.g. splendida*. *L.g. yumensis*, *L.g. conjuncta*, and *L.g. nitida* are considered synonyms of *L.g. californiae*. No new subspecies are described.

1 This work was completed in partial fulfillment for the degree of Doctor of Philosophy at Louisiana State University, Baton Rouge, Louisiana.

INTRODUCTION

Fifty years have elapsed since the publication of Blanchard's (1921) revision of the genus *Lampropeltis*. For that classical study, Blanchard examined 1,581 specimens of the genus, which he considered to be comprised of three natural divisions (excluding the then poorly known *L. mexicana*), the *calligaster, getulus,* and *triangulum* groups. Within the *getulus* group, Blanchard included two species, *L. getulus* and *L. californiae*, and eleven subspecies: *L.g. boylii, L.g. brooksi, L.g. conjuncta, L.g. floridana, L.g. getulus, L.g. holbrooki, L.g. niger, L.g. splendida, L.g. yumensis, L.c. californiae,* and *L.c. nitida*. Subsequently, additional taxa have been described: *Lampropeltis catalinensis* Van Denburgh and Slevin, 1921; *L.g. sticticeps* Barbour and Engels, 1942; *L.g. goini* Neill and Allen, 1949; and *L.g. nigritus* Zweifel and Norris, 1955. Klauber (1936, 1939, 1944) established that *L.c. californiae* and *L.g. boylii* are polymorphic phases of *L.g. californiae*. Schmidt (1953) included *L.g. sticticeps* in the synonymy of *L.g. getulus* without comment, but Wright and Wright (1957) recognized the subspecies as problematical and Lazell and Musick (1973) considered the taxon valid. Duellman and Schwartz (1958) placed *L.g. brooksi* in the synonymy of *L.g. floridana*. Soule and Sloan (1966) included *L. catalinensis* as a subspecies of *L. getulus* without comment.

Since Blanchard's (1921) revision, there has been no analysis of geographic variation in *Lampropeltis getulus*. The status of *L.g. catalinensis, L.g. conjuncta, L.g. goini, L.g. nigritus, L.g. sticticeps,* and *L.g. yumensis* is questionable. Uncertainty clouds the relationships among *L.g. goini, L.g. floridana,* and *L.g. getulus; L.g. niger* and *L.g. getulus*; *L.g. catalinensis* and all other forms; *L.g. nitida* and *L.g. conjuncta*; and the two pattern phases of *L.g. californiae*. The additional specimens that have become available since 1921 in collections throughout the country have made this study not only possible, but desirable, in order to clarify the systematics of the species.

METHODS AND PROCEDURES

During the course of this study I examined 2,200 specimens of *Lampropeltis getulus* from the following collections:

AMNH-American Museum of Natural History; AS-Albert Schwartz, Private Collection; ASDM-Arizona-Sonora Desert Museum; ASU-Arizona State University; AU-Auburn University; BCB-Bryce C. Brown, Private Collection; BS-Bruce Sutton, Private Collection; CAS-California Academy of Sciences; CA-Chicago Academy of Sciences;CM-Charleston Museum; DU-Duke University; EAL-Ernest A. Liner, Private Collection; EVRC-Everglades National Park Reference Collection; FMNH-Field Museum of Natural History; FSU-Florida State University; INHS-Illinois Natural History Survey; ISM-Illinois State Museum; JTC-Joseph T. Collins, Private Collection; KU-University of Kansas Museum of Natural History; LACM-Los Angeles County Museum; LDO-Lewis D. Ober, Private Collection; LDW-Larry D. Wilson, Private Collection; LSUMZ-Louisiana State University Museum of Zoology; LTU-Louisiana Tech University; MCZ-Museum of Comparative Zoology, Harvard; MSU-Mississippi State University; MVC-Museum of Vertebrate Zoology, University of California; NCSM-North Carolina State Museum; NLU-Northeast Louisiana University; NMSU-New Mexico State University; OSU-Oklahoma State University Museum of Natural and Cultural History; PMB-Philip M. Baker, Private Collection; RAT-Robert A. Thomas, Private Collection; SDSNH-San Diego Society of Natural History; SM-Strecker Museum; TCWC-Texas Cooperative Wildlife Collection, Texas A & M; TNHC-Texas Natural History Collection, University of Texas; TTC-Texas Technological College; TU-Tulane University; UAHC-University of Alabama Herpetological Collection; UAZ-University of Arizona; UCM-University of Colorado Museum; UF-University of Florida, Florida State Museum; UG-University of Georgia; UIMNH-University of Illinois Museum of Natural History; UK-University of Kentucky; UM-University of Miami; UMMZ-University of Michigan Museum of Zoology; UNM-University of New Mexico; USA-University of Southern Alabama; USL-University of Southwestern Louisiana; USM-University of Southern Mississippi; USNM-United States National Museum; UT-University of Tennessee.

In addition to the preserved museum specimens, I examined many living specimens in order to increase my understanding of color and pattern variation.

Dorsal scale reduction formulas were recorded as in Dowling (1951a), beginning one head length posterior to the head and ending one head-length anterior to the vent. Ventral scales were counted in the standard manner following Dowling (1951b). Measurements were made in the following manner: snout-vent length, from the tip of the snout to the posterior margin of the anal plate; tail length, from the posterior margin of the anal plate to the tip of the tail (only specimens with entire tail spines were measured); head length, taken in a straight line from the posterior tip of the lower jaw to the tip of the rostral plate; snout length, taken in a straight line from the anterior margin of the orbit to the tip of the rostral plate. All measurements were made on preserved specimens. Unless otherwise noted in the presentation of scutellation data, the figures in parentheses represent the percentage of the specimens examined possessing that character.

Drawings of midbody patterns are composite because it is not possible to depict all pattern variations. Dorsal bands were counted on the body only, beginning one head length posterior to the head and terminating above the vent.

GENUS *LAMPROPELTIS* FITZINGER

Lampropeltis Fitzinger, 1843: 25. Type species, *Herpetodryas getulus* Schlegel.

Sphenophis Fitzinger, 1843: 25. Type species, *Coronella coccinea* Schlegel = *Lampropeltis triangulum* (Lacépède).

Ophibolus Baird and Girard, 1853: 82. Type species *Herpetodryas getulus* Schlegel.

Osceola Baird and Girard, 1853: 133. Type species, *Calamaria elapsoidea* Holbrook = *Lampropeltis triangulum* (Lacépède).

Bellophis Lockington, 1876: 52. Type species, *Coluber zonatus* Blainville.

Oreophis Duges, 1897: 284. Type species, *O. boulengeri* Dugès = *Lampropeltis mexicana* (Garman).

Triaenopholis Werner, 1924: 50. Type species, *T. arenarius* Werner = *Lampropeltis getulus* (Linnaeus).

Definition.—A genus of colubrid snakes with smooth lanceolate dorsal scales in 17 to 27 rows, each scale with 2 apical pits, equal in size except for the slightly enlarged ones in the first or first and second rows; head not or only slightly distinct from neck; eye moderate in size with a round pupil; nasal divided; ventrals not angular; anal plate entire; subcaudals normally divided; tail moderately long; maxillary teeth 12 to 20 and ungrooved; dentary teeth 12 to 18; palatine teeth 8 to 14; pterygoid teeth 12 to 23; hemipenes clavate or bilobed, calyculate apically, spinose on lower distal half, basal half naked or with minute spines, sulcus spermaticus single.

LAMPROPELTIS GETULUS (LINNAEUS)

Coluber getulus Linnaeus, 1766: 382.
Coluber eximis: Harlan, 1827: 360. Misapplication of *C. eximis* Dekay, 1842 = *Lampropeltis t. triangulum.*
Coluber californiae Blainville, 1835: 292.
Coronella sayi: Holbrook, 1842: 99. Misapplication of *Coluber sayi* Schlegel, 1837 = *Pituophis melanoleucus sayi.*
Ophibolus boylii Baird and Girard, 1853: 82.
Ophibolus splendida Baird and Girard, 1853: 83.
Coronella balteata Hallowell, 1853: 236.
Coronella pseudogetulus Jan, 1863: 238, 247.
Lampropeltis conjuncta: Van Denburgh, 1895: 142.
Lampropeltis nitida Van Denburgh, 1895: 143.
Lampropeltis holbrooki Stejneger, 1903: 152.
Lampropeltis boylei: Atsatt, 1913: 41.
Lampropeltis catalinensis Van Denburgh and Slevin, 1921: 397.
Triaenopholis arenarius Werner, 1924: 50. Based on a bleached specimen without data (M.A. Smith, 1928).

Holotype.—None designated. Type locality originally given as "Carolina" but Klauber (1948) restricted it to the vicinity of Charleston, South Carolina.

Definition.—A medium to large-sized (to 2083 mm) species of *Lampropeltis* characterized by a tail 10.8 to 15.3% of total length in males, 9.2 to 14.7% in females; temporals normally 2 + 3; oculars 1 + 2; loreal usually present; supralabials usually 7; infralabials 9 or 10; intergenials 1 + 2, 2 + 2, or 2 + 3; dorsal scales in 19 to 25 rows at midbody; ventrals 197 to 250 in males, 198 to 255 in females; subcaudals 44 to 63 in males, 37 to 57 in females; teeth 12 to 16 on each maxilla, 14 to 17 on each dentary, 8 to 11 on each palatine, and 12 to 20 on each pterygoid; hemipenis slightly to distinctly bilobed; dorsal pattern highly variable, but basically consisting of a black to chocolate brown ground color, often with some or all of the scales light or light centered (white, cream, or occasionally reddish yellow), frequently forming distinct crossbands or sometimes longitudinal stripes; venter also highly variable, ranging from uniformly dark to uniformly light.

Range.—North America, from the Atlantic Coast below the 41st Parallel to the Pacific Coast below the 43rd Parallel, and south into Mexico to Zacatecas and San Luis Potosi, and most of the Baja California peninsula (conspicuously absent from Colorado, the northern one-third of New Mexico, northeastern Arizona, most of Utah, and northeastern Nevada); vertical range from sea level to about 2,100 m.

Relationships.—*Lampropeltis getulus* is a generalized snake that represents one of probably four lines of radiation from a primitive stock closely allied to the group of colubrine genera that includes *Pituophis* and *Elaphe*. On the basis of fossil records (see p. 97), I suggest that this radiation occurred during the early Pliocene. Further, on the basis of the presence of characters considered to be primitive within the species, I consider northern Mexico and the adjacent south-central United States to be the area where this radiation initially occurred. This centrally located region offers the greatest theoretical potential for derivation of most populations of *L. getulus* and other species in the genus.

The species most closely related to *Lampropeltis getulus* is *L. calligaster* which differs only in pattern, the latter being a distinctly blotched snake. Both of these species differ from members of the *triangulum* and *mexicana* groups of kingsnakes in not having the posterior two maxillary teeth enlarged. However, Webb (1961) suggested that on the basis of similarity in color pattern, *L. calligaster* might be a derivative of the *mexicana* group. He further stated that *L. getulus* might be a derivative of *L. calligaster,* although "no living forms indicate relationships." This line of reasoning based on a single character state is unwarranted. Although I do regard the blotched pattern as more primitive than the speckled, banded, or striped patterns exhibited by *L. getulus*, I suggest that the pattern of *L. calligaster* represents retention of a primitive character, and that the pattern of *L. getulus* is a specialization. *L. calligaster* exhibits such specializations as reduced head size and, in *L.c. rhombomaculata*, as reduced scutellation (dorsal scale rows, infralabials); these are modifications for a more fossorial existence.

I suggest, therefore, that the initial radiation of *Lampropeltis* consisted of two lines of divergence, the *getulus* and *triangulum* groups. The *getulus* group differentiated into *L. getulus* and *L. calligaster* whereas *L. triangulum, L. pyromelana, L. zonata,* and *L. mexicana* evolved from the primitive stock of the *triangulum* group.

Fossil history.—Pleistocene fossils of *Lampropeltis getulus* have been reported from various localities in Florida (Auffenberg, 1963; Brattstrom, 1953a; Holman, 1958), Texas (Holman, 1964a), Nebraska (Holman, 1964b), Nevada (Brattstrom, 1954), and California (Brattstrom, 1953b and c). These widely separated localities suggest that the species has been in existence for a considerable length of time, at least during the entire Pleistocene and probably back into the Pliocene. The genus is represented in the Pliocene of Nebraska, Kansas, Oklahoma, and Michoacan, Mexico (Brattstrom, 1955 and 1967; Holman, 1964a).

VARIATION

Individual Variation.—The degree of individual variation within a closely interbreeding population is usually quite small. For example, in the number of ventral scales, the range of variation within a single population usually does not exceed 12 scales (*i.e.*, 201-211 for 10 males from Cameron Parish, Louisiana; 201-212 for 25 males from the vicinity of New Orleans, Louisiana).

Supralabials usually are 7 (97.1%), but a few individuals have 8 (2.5%) or 6 (0.4%). Infralabials are somewhat less consistent and some geographic variation is noted, but 9 is the most frequently encountered number (80.8%), sometimes 10 (17.5%), rarely 8 (1.3%) or 11 (0.4%). Temporals are normally 2 + 3 (94.5%) but aberrant individuals may possess 2 + 2 (2.0%), 2 + 1 (0.05%), 2 + 4 (1.9%), 3 + 3 (0.05%), 3 + 4 (0.7%), 1 + 2 (0.4%), or 1 + 3 (0.3%). Oculars are the most consistent scales in that 99.3% of the specimens examined possess 1 + 2, but formulas of 1 + 3 (0.3%), 1 + 1 (0.2%), or 2 + 2 (0.2%) do occur. The loreal is normally present, but in an occasional specimen the scale may be absent on either or both sides of the head. This condition most often results from fusion of the loreal with the supraocular, preocular, or postnasal, but in 2% of the specimens examined, no loreal was found and no evidence of fusion was noted. Usually, the postnasal and preocular extend to fill in this area. Many individuals were found in which the loreal was represented by a greatly reduced, almost granular scale. A female specimen (KU 74114 from Cumberland County, Tennessee) lacks the loreal on both sides, and within her brood of seven, four specimens also lack the loreal scale. This evidence indicates that a single allele may be responsible for the absence of a loreal scale. All specimens examined, except one, possess a single anal plate.

There is considerable individual variation in proportional characters. Relative tail length varies from the mean by several per cent in every sample. Head length as a percentage of snout-vent length varies within about one-half per cent of the mean for any given length (Fig. 1). The range of variation of snout length relative to head length is as much as $\pm$ 7% from the mean (Table 1). Some of this variation is undoubtedly due to the inherent difficulty of measuring preserved snakes.

Ontogenetic Variation.—Character changes from the juvenile to the adult can be detected in relative head length, to a lesser degree in relative tail length, and, in some areas, in pattern.

Marked differences are found in head length of newly hatched individuals (up to 5.7% of snout-vent length), when com-

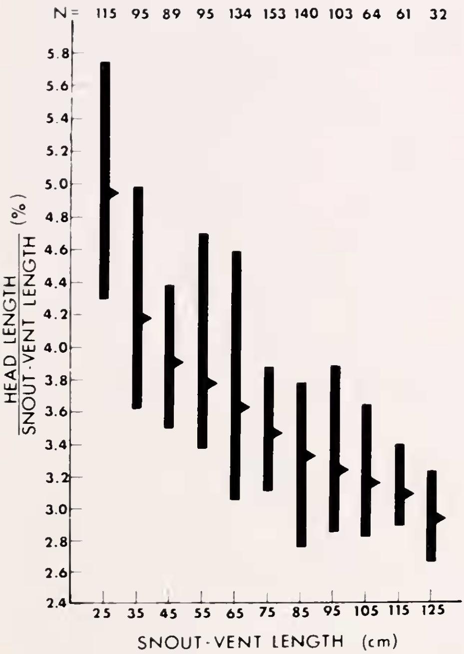


Figure 1. Ontogenetic variation in head length expressed as a percentage of snout-vent length in *Lampropeltis getulus*. The mean for a sample of any given snout-vent length is indicated by a point on the sample range.

pared with adults (as little as 2.7% of snout-vent length). This condition is apparently due to allometric growth of the body and the head (Fig. 1).

Tail length varies ontogenetically only slightly. Newly hatched individuals tend to have slightly longer tails, and very large adults (>1150 mm) tend toward a proportionally shorter tail, but the differences are within the extremes of individual variations at any length.

Ontogenetic pattern variation is found in certain geographic areas. In the central and eastern portion of the range (southern Iowa to eastern Texas east to Ohio to northwestern Georgia and Alabama), juveniles have distinct light dorsal bands on a dark background with little or no spotting between the bands. As the individual matures, one of two changes occurs. In the western portion of the area outlined above, some or all of the dorsal scales develop a light center which I shall refer to as secondary spotting. This secondary spotting may completely obscure the juvenile dorsal bands (especially in Missouri, western Arkansas, eastern Oklahoma, eastern Texas, and portions of Louisiana), or they may remain evident. In the eastern portion of this range (Illinois, Indiana, Ohio south to northeastern Alabama and northwestern Georgia), the reverse ontogenetic change occurs. The juvenile pattern becomes reduced in the adult, sometimes resulting in an almost complete loss of any evidence of dorsal bands or secondary spotting, leaving a black dorsum with the minute spots on some scales forming vague dorsal bands.

In the southern half of the Florida peninsula, individuals exhibit a similar form of ontogenetic pattern variation. Juveniles are patterned with distinct dorsal bands, 1.5 to 4 scales long, which usually do not reach the first or second scale row, often ending abruptly or sometimes forking laterally and joining neighboring bands. As the animal matures, scales between the dorsal bands develop a light spot at the anterior end. These secondary spots expand until the entire scale, except the most posterior edge, is light colored. The juvenile pattern may be completely obscured in the adult.

Sexual Variation.—Sexual dimorphism is found in several characters. In some populations, there is a difference between males and females in the number of ventral scales. In about half of these populations, the female has a slightly higher number; in the other populations, the reverse is true. The average difference between males and females is never more than five ventral scales. Many populations, especially in extreme southeastern United States, exhibit no sexual variation in this character.

Subcaudals vary sexually, with females having consistently fewer, although the degree of difference varies geographically. Similarly, females possess a proportionally shorter tail than males.

Table 1. Sexual and geographic variation in snout length expressed as a percentage of head length. Numbers in parentheses indicate range of variation.

Geographic range	males	females
Southern Florida	31.3 (29.6—33.8) N= 17	30.7 (29.3—32.6) N= 19
Virginia to New Jersey south to northern Florida	29.9 (26.8—34.0) N= 109	29.9 (26.7—33.1) N= 62
Illinois to Ohio south to northern Alabama and northwestern Georgia	30.2 (27.0—32.3) N= 43	31.1 (29.4—33.6) N= 20
Southern Iowa south to eastern Texas, Louisiana, Mississippi and western Alabama	30.4 (27.7—34.0) N= 145	30.9 (28.4—34.2) N= 105
Eastern Arizona east to western Texas and south through Mexico	30.5 (27.9—32.2) N= 36	31.2 (29.4—33.2) N= 16
Oregon, Nevada, Utah south to western Arizona and Baja California	31.1 (27.9—33.7) N= 114	30.7 (28.3—33.8) N= 97

Snout length relative to head length varies to some extent sexually and geographically (Table 1). All of these figures, however, may be of little significance because of the amount of individual variation. Head length does not vary sexually.

Geographic Variation.—Geographic variation is found in the number of ventrals, subcaudals, infralabials, intergenials, and dorsal scale rows, the size and shape of the loreal, the relative size of the anterior and posterior genials, color pattern, and structural features of the hemipenes. Proportional characters also vary geographically, but their significance is slight.

Ventrals—The geographic variation of ventral scales is summarized in Figs. 2a, 2b and 3. In general, the greatest number of ventrals is found in southern California and Baja California (213-255), the number decreasing to the north and east. Areas in which the snakes have a low number of ventrals are in the Chihuahuan Desert of Mexico (199-216); western Louisiana, southeastern Texas, Arkansas, eastern Oklahoma, eastern Kansas, Missouri, Illinois, Indiana, Ohio, Kentucky, and Tennessee (197-214); and the extreme northeastern coastal portion of the range, including the islands off North Carolina (200-211). Over the remainder of the range of the species, the range of variation is between 210 and 225.

A series of specimens from Mexico is problematical. The majority of specimens examined from Durango, Zacatecas, and San Luis Potosí have a low number of ventrals (200-205). Two specimens, however, have an unusually high number of ventrals. A female from 29 miles NE of Ciudad Durango (EAL 1850) has 237 ventrals compared with a male from 5.1 miles east-southeast of Durango (UMMZ 114654) which has only 203 ventrals. Similarly, a male from 4.6 miles S of San Lorenzo, San Luis Potosi (EAL 552) has 227 ventrals, whereas four

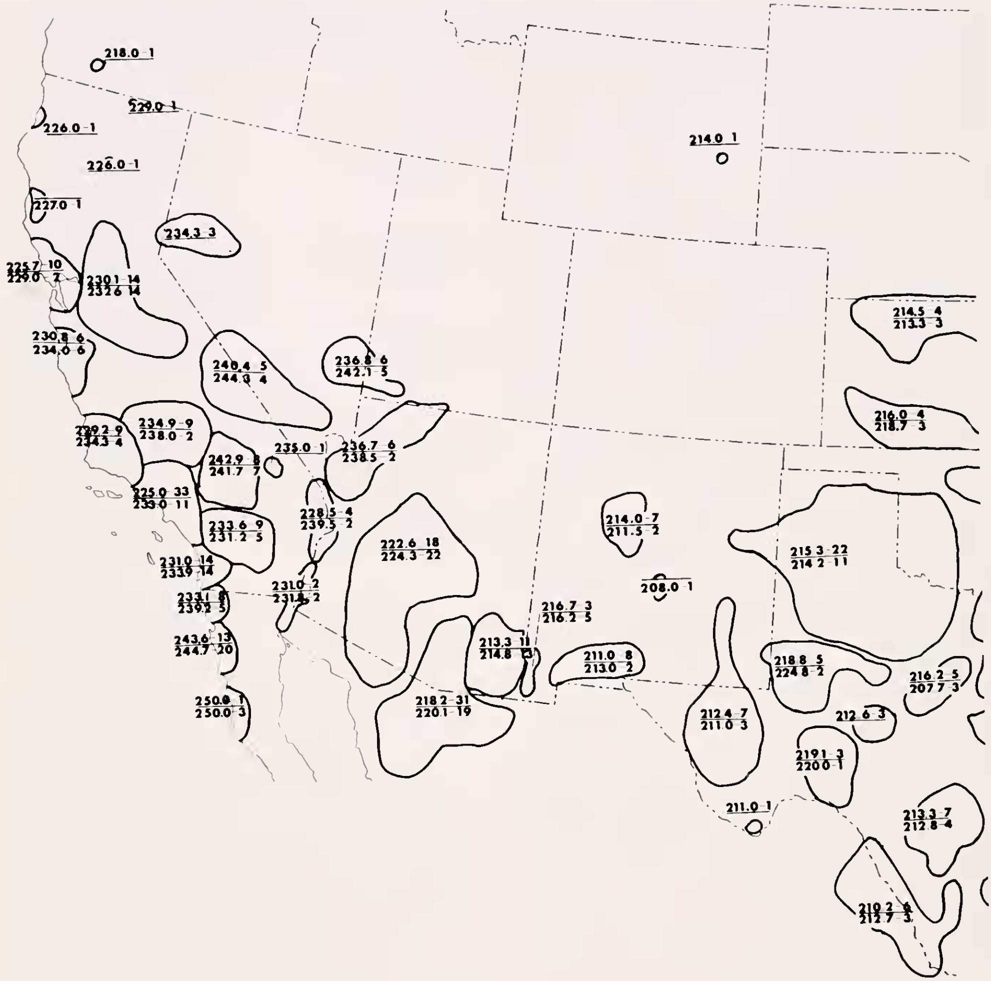


Figure 2a. Geographic variation in the number of ventral plates in *Lampropeltis getulus* in the western United States. The upper figures associated with each sample represent the mean and the sample size (separated by a dash) for males; lower figures present the same data for females. Data are not indicated separately when the mean for males and females is identical.

specimens from nearby localities have between 200 and 205.

Subcaudals—Geographic variation in subcaudal number is shown in Figs. 4 and 5. The amount of individual variation is greater than the geographic variation, but certain tendencies are noted. Specimens with the greatest number of subcaudals are found in the western United States where the maximum is 63 in males and 57 in females. The averages range from 52.6 to 57.2 in males and 48.0 to 52.7 in females. The average number of subcaudals reduces to a low of 46.2 in males and 40.5 in females in the northeastern part of the range (Maryland and Delaware). Clinal variation is noted in the Atlantic coastal populations, where there is a general increase from north to south. The New Jersey population,

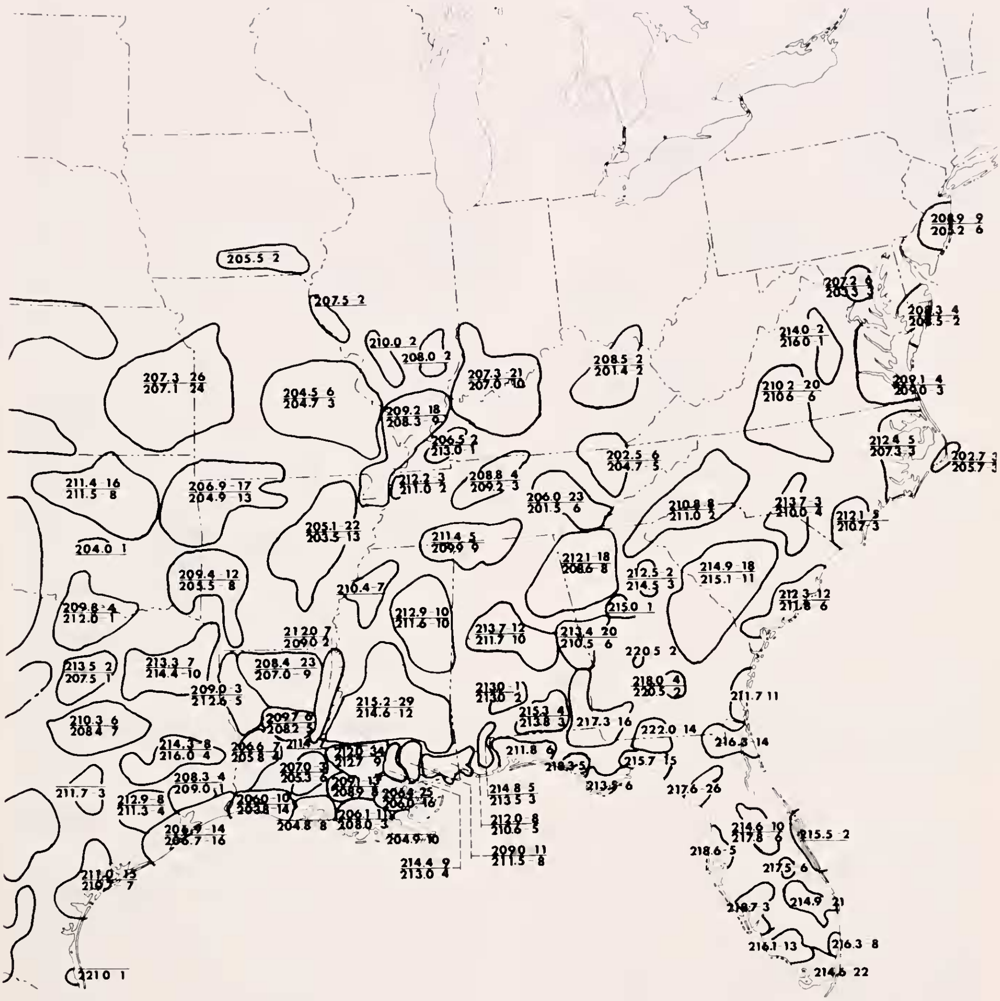


Figure 2b. Geographic variation in the number of ventral plates in *Lampropeltis getulus* in the eastern United States. Explanation as for Figure 2a.

however, is unusual in that the males average 2.9 subcaudals more than the Maryland and Delaware populations; females 2.1 subcaudals more.

Surprisingly, there is no correlation between the number of subcaudals and relative tail length. The western populations, despite having a higher number of subcaudals, have about the same tail length/total length ratio as the remaining populations. The differences in number that do exist appear to be determined by the size of the subcaudal scales, not by the length of the tail.

Infralabials—Among eastern and central populations, infralabials vary individually. The majority of specimens have 9 (80 - 90%), the remainder 10 (10 - 20%) or rarely 8 or 11. In the extreme western portion of the range (Oregon, Nevada, Utah, northern and western Arizona, California, and Baja California), only 66.8% of the specimens examined possess 9 infralabials, while

Figure 3. Geographic variation in the number of ventral plates in *Lampropeltis getulus* in Mexico. See Figure 2 for explanation.

30.8% have 10. The majority of specimens examined from the Baja Peninsula have 10 infralabials: 62.5% from Baja California del Sur; 56.0% from Baja California del Norte. The percentage declines abruptly to only 30.0% in southwestern California (San Diego, Orange, and Los Angeles counties).

Loreal—The shape of the loreal varies individually and geographically. In most specimens, the loreal is square (45.0%), slightly longer than high (10.2%), or slightly higher than long (9.2%). The loreal is considerably longer than high in 18.7% of the specimens examined, and considerably higher than long in 14.9%.

Geographic variation in loreal shape is summarized in Table 2. The most apparent geographic tendencies are seen in peninsular Florida where 71.0% of the specimens examined have a loreal that is higher or slightly higher than long, whereas this condition prevails in only 46.0% of the specimens in Atlantic coastal populations. By comparison, however, fewer specimens from adjacent areas have a high loreal.

In the extreme western United States and Baja California, the loreal is usually slightly longer or much longer than high (60.0%). In New Mexico, western Texas, and Central Mexico, only 44.7% of the specimens have a long loreal. In southern Arizona and adjacent Mexico, however, only 32.2% of the specimens have a long loreal.

Genials—The relative size of the genials varies geographically. In Atlantic coastal populations, the anterior and posterior genials are usually equal in length (62.3%), or the anterior genials are only slightly longer (13.0%) or slightly shorter (9.2%). In central populations, only 31.4% of the specimens examined have genials of equal length, whereas in 46.8% the anterior genials are very much longer than the posterior genials (posterior genial length/anterior genials are slightly longer. Among these central populations, specimens from New

Mexico, eastern Mexico, Texas, western Oklahoma and Kansas have longer anterior genials (54.0%) than the eastern populations (44.1%), with the lowest percentage (32.2%) in Illinois, Indiana, Ohio, Kentucky and Tennessee. In the extreme western states and Baja California, 52.3% of the specimens examined have the anterior genials much longer than the posterior, and in another 26.3% the anterior genials are slightly longer. In only 21.2% of the specimens are the genials equal.

Intergenials—The relative size of the genials is correlated with the number of intergenials. Among eastern populations, most individuals have a combination of 1 + 2 intergenials between the posterior genials (82.0%) with most of the remaining having only 2 intergenials (10.4%). Genials in these specimens are generally about equal in length.

Specimens from western Texas, New Mexico, eastern Arizona, and Mexico (except Baja California) usually have an intergenial arrangement of 2 + 2 (62.0%) or 2 + 3 (22.2%), the latter being especially true in the western-most areas. Individuals from central and northern Texas, western Oklahoma, and Kansas are variable in that 59.4% of the specimens examined have 1 + 2 intergenials, 35.5% have 2 + 2, and 3.9% have only 2. The specimens with a greater number of intergenials normally have short posterior genials.

Pacific coastal states and Baja California populations normally have 2 + 3 (55.0%) intergenials or 2 + 2 (38.0%). Only 1.8% of the specimens examined from those areas have 1 + 2 intergenials.

Dorsal scale rows—The number of dorsal scale rows at midbody varies from 19 to 25 or, rarely, 27. Generally, specimens from east of the Great Plains to the Atlantic coast, except peninsular Florida, have a maximum of 21 dorsal scale rows with typical reductions as follows:

$$21 \frac{4 + 5\ (111\text{-}177)}{4 + 5\ (116\text{-}176)} 19 \text{ or,}$$

$$19 \frac{+6\ (25\text{-}63)}{+6\ (25\text{-}63)} 21 \frac{4 + 5\ (111\text{-}146)}{4 + 5\ (116\text{-}145)} 19.$$

Occasionally, specimens may reduce to 7 scale rows anterior to the vent:

$$19 \frac{+6\ (28\text{-}63)}{+6\ (30\text{-}63)} 21 \frac{4 + 5\ (98\text{-}137)}{4 + 5\ (102\text{-}139)}$$

$$19 \frac{4 + 5\ (164\text{-}197)}{4 + 5\ (176\text{-}198)} 17, \text{ or}$$

$$21 \frac{4 + 5\ (100\text{-}140)}{4 + 5\ (101\text{-}138)}$$

$$19 \frac{5 + 6\ (165\text{-}193)}{5 + 6\ (163\text{-}195)} 17.$$

One specimen, LSUMZ 23508 from 2 miles S Holmwood, Calcasieu Parish, Louisiana, has a maximum of only 19 scale rows and reduces to 17 as follows:

$$19 \frac{4 + 5\ (148)}{4 + 5\ (151)} 17\ [206].$$

Rarely, specimens may reach the maximum of 23 scale rows by the addition of a sixth row on each side, as in DU R-293 from 10 miles NW Durham, Durham County, North Carolina:

$$21 \frac{+6\ (60)}{+6\ (59)} 23 \frac{6 + 7\ (103)}{5 + 6\ (109)}$$

$$21 \frac{4 + 5\ (176)}{4 + 5\ (178)} 19\ [215].$$

In general, those specimens from the western portion of the range outlined above (Kansas south to Texas and east to Ohio south to Alabama) tend to reduce to 19 scale rows farther anteriorly, and more frequently reduce to 17 one head length anterior to the vent than Atlantic coastal specimens, which tend to reduce to 19 scale rows farther posteriorly and rarely reduce to 17. Occasional individuals, for example NCSM 5729 from Raleigh, Wake County, North Carolina, may reduce from 21 to 19 scale rows by the fusion of scale rows 3 and 4 instead of 4 and 5:

$$21 \frac{3 + 4\ (159)}{3 + 4\ (161)} 19\ [211].$$

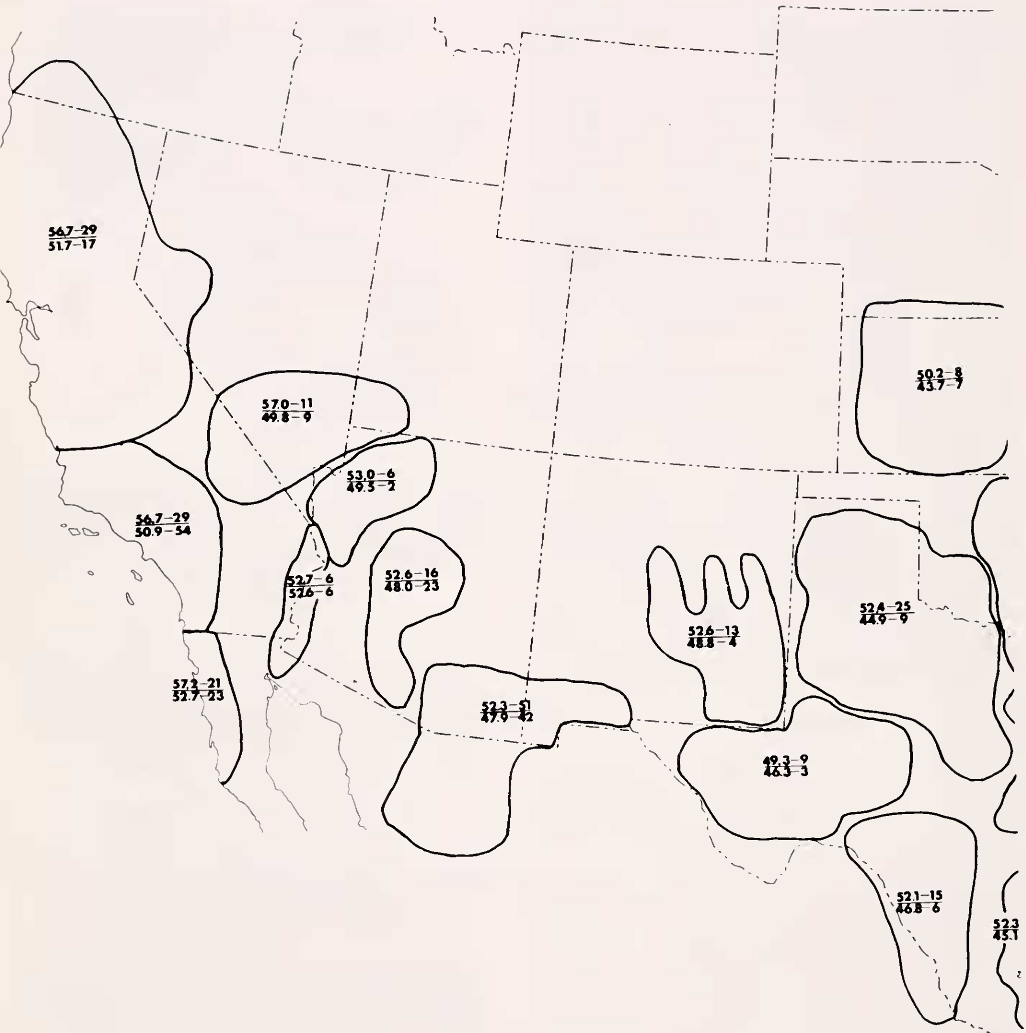


Figure 4a. Geographic variation in the number of subcaudals in *Lampropeltis getulus* in the western United States. See Figure 2 for explanation.

Also, occasional specimens will increase from 19 to 21 scale rows anteriorly by the addition of row 5 on both sides, instead of row 6, as, for example, in DU R-29 from 2 to 3 miles N Hillsboro, Orange County, North Carolina:

$$19 \frac{+5\ (29)}{+5\ (25)}\ 21 \frac{4\ +\ 5\ (146)}{4\ +\ 5\ (145)}\ 19\ [212].$$

A posterior reduction to 17 scale rows involves either the fusion of rows 4 and 5 or 5 and 6 and only rarely rows 3 and 4.

In southern Florida, specimens usually have a maximum of 23 scale rows. Anteriorly, the number of scale rows may be 21, as exemplified by an EVRC uncatalogued specimen from Flamingo Campground, Everglades National Park, Monroe County, Florida:

$$21 \frac{+6\ (46)}{+6\ (43)}\ 23 \frac{5\ +\ 6\ (139)}{5\ +\ 6\ (132)}$$

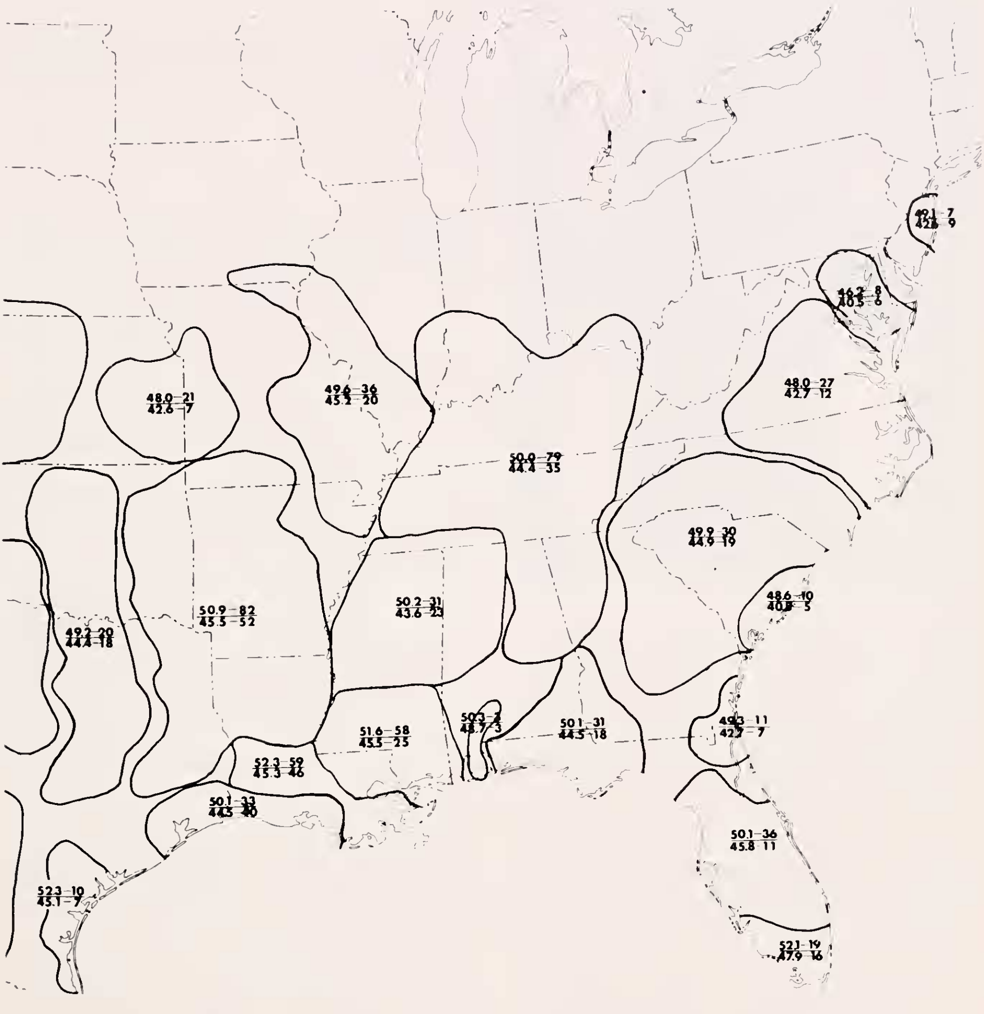


Figure 4b. Geographic variation in the number of subcaudals in *Lampropeltis getulus* in the eastern United States. See Figure 2 for explanation.

$$21 \frac{4 + 5\ (184)}{4 + 5\ (183)} 19\ [220],$$

or, may be 23, as in AS 771 from Miami, Dade County, Florida:

$$23 \frac{5 + 6\ (122)}{4 + 5\ (116)} 21\ [217].$$

The reduction to 19 scale rows occurs within 40 ventrals of the vent; when the reduction occurs within one head length of the vent it is not included in the reduction formula. The reduction from 23 to 21 rows is usually due to fusion of rows 6 and 7 or 5 and 6, but may be 4 and 5.

Specimens from the western United States and northern Mexico are similar in their scale reductions, but many individuals have a maximum of 25 scale rows, as for example UMMZ 102436 from 4 miles NE Chiricahua, Cochise County, Arizona:

$$25 \frac{6 + 7\ (137)}{6 + 7\ (138)} 23 \frac{5 + 6\ (175)}{5 + 6\ (164)} 21\ [221].$$

Figure 5. Geographic variation in the number of subcaudals in *Lampropeltis getulus* in Mexico. See Figure 2 for explanation.

Occasional specimens have 27 dorsal scale rows as TCWC 12592 from 3 miles S Navajoa, Sonora, Mexico:

$$25\,\frac{+\,13\ (73)}{}\,26\,\frac{12\ +\ 13\ (77)}{}$$

$$25\,\frac{+\,13\ (83)}{+\,13\ (102)}\quad 27\,\frac{5\ +\ 6\ (136)}{5\ +\ 6\ (136)}$$

$$25\,\frac{12\ +\ 13\ (137)}{11\ +\ 12\ (149)}\,23\,\frac{6\ +\ 7\ (170)}{5\ +\ 6\ (172)}$$

$$21\ [219].$$

The final reduction from 23 to 21 scale rows is usually more posterior in the western populations than in Florida specimens; in specimens from California and Baja California, the reduction is even farther posterior than in Texas specimens. This phenomenon is correlated with the higher number of ventral scales found in the extreme western part of the range. For example, TNHC 8348 from 15 miles S Sheffield, Terrell County, Texas, reduces to 21 at the level of ventrals 125 to 130:

$$23\,\frac{+\,7\ (60)}{+\,7\ (62)}\,25\,\frac{5\ +\ 6\ (107)}{5\ +\ 6\ (89)}$$

$$23\,\frac{6\ +\ 7\ (130)}{5\ +\ 6\ (125)}\,21\ [218],$$

and LSUMZ 10313 from 4 miles S Uvalde, Uvalde County, Texas, which reduces between ventrals 137 and 140:

$$23\,\frac{6\ +\ 7\ (140)}{6\ +\ 7\ (137)}\,21\ [211].$$

In comparison, CM 55.203.2 from St. George, Washington County, Utah, reduces to 21 rows at the level of ventrals 164 to 166:

$$23\,\frac{6\ +\ 7\ (164)}{5\ +\ 6\ (166)}\,21\,\frac{4\ +\ 5\ (225)}{4\ +\ 5\ (224)}\,19\ [244],$$

or, at the lower extreme, UNM 6691 from Santa Rosa, Sonoma County, California, which reduces at ventral 146:

$$23\frac{6 + 7\ (146)}{6 + 7\ (146)}21\frac{4 + 5\ (200)}{5 + 6\ (207)}19\ [222].$$

The kingsnakes from central Texas, western Oklahoma, and Kansas are intermediate between eastern and western populations, individuals in the sample having a maximum of 23 or 21 rows.

Hemipenes.—Hemipenial morphology varies in two respects, overall shape and number of spines on the proximal half. The everted hemipenis is a moderately bilobed structure with the sulcate lobe slightly longer. Male specimens from the Atlantic coastal states, including all of Florida and southeastern Alabama, have deeply bilobed hemipenes with the distal end greatly expanded laterally (Fig. 6,A). This expansion results in a maximum width averaging 75% (68-89%) of the exposed length when fully everted. Throughout the remaining portion of the range of *Lampropeltis getulus*, except the Pacific coastal states of Nevada, Utah, and western Arizona, the hemipenis is not expanded distally, the width averaging 58% (48-68%) of the length. Specimens in the eastern portion of this area (eastern and northern Alabama, Mississippi, Louisiana, Arkansas, eastern Texas, and eastern Oklahoma) have a more clavate organ averaging 52% (49-66%) of the length (Fig. 6,B). Specimens from Texas to southeastern Arizona have a comparatively slightly expanded organ (Fig. 6,C) and the hemipenes of Pacific coastal specimens are moderately expanded (Fig. 6,D).

Throughout most of the range of the species, the basal portion of the hemipenis is naked or ornamented with a few small scattered spines. In eastern Louisiana and southern Mississippi, however, the basal portion of the organs of some individuals is densely covered with minute spines (Fig. 6,B).

Pattern.—The dorsal color pattern is the most significant aspect of geographic variation in *Lampropeltis getulus*. There are three basic patterns with major variations and modifications of these: 1) the speckled pattern, 2) the longitudinally striped pattern, and 3) the banded or "ringed" pattern.

Figure 6. Geographic variation in hemipenial morphology in *Lampropeltis getulus*: A. NCSM 5175 from 4¾ miles NW Laurel Hill, Scotland County, North Carolina; B. Baton Rouge, East Baton Rouge Parish, Louisiana (specimen not available); C. LSUMZ 9995 from 8 miles E Tucson, Pima County, Arizona; D. LSUMZ 9246 from Smoke Creek, Washoe County, Nevada.

The speckled pattern consists of a dark ground color with each scale on the lateral 8 to 10 rows containing a light central area. Occasional scales in the median 5 to 9 rows are also light-centered with the light spots oriented laterally to form a series of 42 to 97 distinct narrow bands across the dorsal surface (Fig. 7,A). This pattern is found in western Texas, New Mexico, eastern Arizona, and Mexico from Chihuahua and Sinaloa east to Veracruz.

A modified speckled pattern in found in eastern Texas, Louisiana, Arkansas, eastern Oklahoma, Missouri, western Illinois, Mississippi, and southern Alabama. Specimens from this area exhibit a pattern in which every scale, or almost

Table 2. Geographic variation in loreal shape expressed as a percent of specimens examined.

	Loreal Shape:	Square	Slightly longer	Slightly higher	Longer	Higher
New Jersey to Virginia south to northern Florida and southeastern Alabama	N= 211	45.5	1.4	12.3	6.2	33.6
Peninsula Florida	N= 62	27.4	1.6	16.2	0	54.8
Eastern Illinois to Ohio south to northwestern Georgia and northeastern Alabama	N= 112	50.9	3.6	11.6	11.6	17.0
Southern Illinois, extreme western Tennessee, north-central and northwestern Alabama	N= 47	42.6	17.0	23.4	4.3	12.7
Southwestern Alabama, Mississippi, Louisiana, Arkansas, Missouri, eastern Oklahoma, and eastern Texas	N= 316	53.5	8.6	12.3	11.1	12.5
Kansas, central and western Oklahoma, northern and central Texas	N= 130	62.3	9.2	8.5	12.3	7.7
Western Texas west to southeastern Arizona, and south to San Luis Potosi and Zacatecas, Mexico	N= 95	38.4	22.6	7.4	22.1	9.5
South-central Arizona, northern Sonora, Mexico	N= 87	49.4	18.4	4.6	13.8	11.5
Baja California, California, Oregon, Nevada, eastern and northern Arizona, Utah	N= 343	33.1	15.5	3.1	44.5	1.2

every scale, has a centrally located light spot. Some of the dorsal scales may have light spots that are irregularly expanded laterally to form 39 to 94 cross bands (Fig. 7,B). In Illinois, Indiana, Ohio, Kentucky, Tennessee, northeastern Alabama, and northwestern Georgia, the pattern described above is reduced due to ontogenetic loss of the scale spotting. The dorsal bands, consisting of a series of spots, are usually retained, however, although the light centers are often very much reduced (Fig. 7,C).

A similar change occurs in the pattern type found in Sonora, Mexico, which is a reduction of the pattern (Fig. 7,A) found in western Texas, New Mexico, eastern Arizona, and the remaining portions of Mexico. Many of the individuals in this area, especially in southern Sonora, loose all traces of the basic pattern and are uniformly black (Fig. 7,D).

Many specimens from Baja California and California, especially southwestern California, are longitudinally striped. There is usually a continuous light vertebral stripe occupying the vertebral scale row and half of each of the paravertebral rows on a dark ground color. The lateral scale rows, especially rows 1 and 2, are almost completely light, forming lateral stripes (Fig. 7,E). Specimens with this pattern are found sympatrically with banded individuals discussed below.

The third basic pattern consists of light dorsal crossbands on a dark ground color. These bands are usually uninterrupted and not made up of a series of spots as are the bands discussed above (Fig. 7,C). Specimens from the eastern coastal states usually have a pattern of bands which begin on scale row 5 and may be connected with adjacent bands by lateral forking (Fig. 7,F). In southern Florida, this pattern is masked by ontogenetic spotting of the dorsal scales between the light bands (Fig. 7,G).

The banded pattern found in Baja California, California, Oregon, Nevada, Utah, and western Arizona differs in that the bands always extend at least to the first dorsal scale row and usually to the venter (Fig. 7,H).

Geographic variation in the number of dorsal bands occurs in both eastern and western banded populations. In the east, the lowest number of dorsal bands is found among specimens from southern Georgia, southeastern Alabama, and northern Florida (18-22). The number increases clinally both northward and

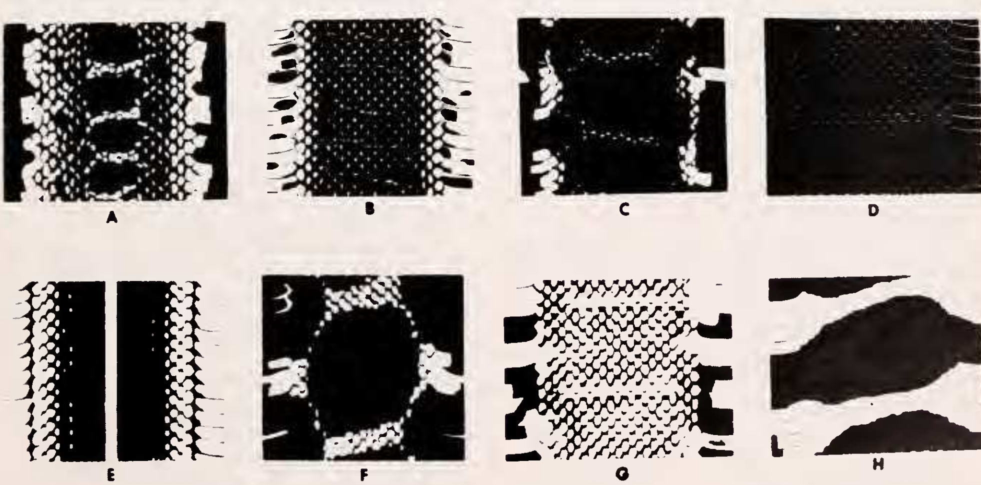


Figure 7. Basic pattern types of *Lampropeltis getulus*. See text (pattern variation) for explanation.

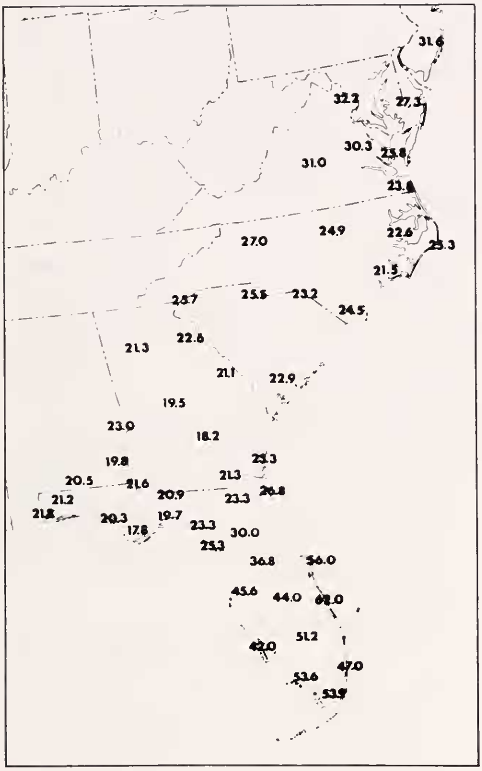


Figure 8. Geographic variation in the number of dorsal body bands in *Lampropeltis getulus* in eastern United States.

southward, increasing to an average of 31.6 in New Jersey, and 53.9 in southern Florida (Fig. 8). In addition, the piedmont populations in North Carolina and Virginia have higher average numbers of dorsal bands (27-32) than coastal populations (21-26).

In the western North American banded populations, the variation in dorsal band number is not as extreme as in eastern populations. Montane populations average generally higher (35-38) than lowland populations (27-30). Clinal variation occurs with the lower numbers in the south, increasing somewhat to the north (Fig. 9).

Non-morphological characters.—Geographical variation in the plasma protein patterns of *Lampropeltis getulus* has been demonstrated by Dessauer and Fox (1958). Specimens from California show a different pattern than a sample from southeastern United States (a mixed sample from Georgia, Mississippi, Louisiana, and Arkansas).

RECOGNITION OF INFRASPECIFIC DIVISIONS

The geographic variation exhibited by *Lampropeltis getulus* in characters of pattern, hemipenial morphology, dorsal scale reduction, loreal shape, intergenial number, and genial size enables the recognition of eight distinct infraspecific divisions, seven of which are allopatric. I recognize these seven allopatric divisions as subspecies of *Lampropeltis getulus*, all of which have available names: *L.g. californiae* (Blainville), *L.g. floridana* Blanchard, *L.g. getulus* (Linnaeus), *L.g. holbrooki* Stejneger, *L.g. niger* (Yarrow), *L.g. nigritus* Zweifel and Norris, and *L.g. splendida* (Baird and Girard). Distribution of these subspecies is summarized in Figs. 10 and 11.

These subspecies exhibit two types of evolutionary relationships to one another. The first is considered to be a primary relationship (*sensu* Eaton, 1970) in which the subspecies have become differentiated but have not entirely lost contact. Where contact still exists, series of demes intermediate in characteristics are found between the adjacent subspecies. Specimens from these populations are considered to be intergrades. Wide zones of intergradation exist between *L.g. getulus* and *L.g. floridana*, *L.g. niger* and *L.g. holbrooki, L.g. holbrooki* and *L.g. splendida*, and *L.g. splendida* and *L.g. nigritus*.

Secondary relationships are those in which subspecies have been separated for a long time and have regained contact. A secondary relationship is characterized by a narrow zone of intergradation, as between *L.g. splendida* and *L.g. californiae*, or the occurrence of only occasional intermediates in nature, as between *L.g. getulus* and *L.g. niger*, and between *L.g. getulus* and *L.g. holbrooki*. On the basis of these secondary relationships, the basic pattern types, and hemipenial morphology, three groups of subspecies can be recognized: the *getulus* complex, consisting of *L.g. getulus* and *L.g. floridana*; the *splendida* complex, consisting of *L.g. splendida, L.g. nigritus, L.g. holbrooki,* and *L.g. niger;* and the *californiae* complex, consisting of only *L.g. californiae.*

KEY TO THE SUBSPECIES OF ADULT *LAMPROPELTIS GETULUS*

1. Maximum number of dorsal scale rows 21 or less................................2
   Maximum number of dorsal scale rows 23 or more..............................4
2. Dorsal coloration black or brown with continuous light bands (1 to 10 scales wide) reaching the venter or forking laterally at the level of scale rows 3 to 6, or stopping abruptly at this level; hemipenis deeply bilobed and expanded laterally.............*getulus*
   Dorsal coloration black with some scales centered with yellow, cream, or white; hemipenis not bilobed or much expanded laterally............. 3
3. Most dorsal scales centered with yellow, cream, or white, the spots on scale rows 6 to 15 sometimes expanded laterally to form narrow light dorsal crossbands............*holbrooki*
   ....
   Dorsum predominantly black, some lateral scales centered with cream or white; often some dorsal scales centered with light pigment to form dorsal bands consisting of a series of spots................................*niger*
4. Light transverse dorsal bands extend laterally to, and often onto, the venter; no spotting between bands........ ....*californiae*
   Dorsal pattern variable, of longitudinal stripes, spotted scales, or uniformly dark......................................5
5. Dorsum dark with a light vertebral stripe and lateral stripes formed by a series of light-centered scales on rows 1 to 3 or 1 to 6; venter usually uniformly light or dark.................. ....*californiae*
   Dorsum without longitudinal stripes..... 6
6. Dorsum uniformly black or with only minute light centers on the lateral scales............................*nigritus*
   Dorsum with scales cream or yellow...7
7. Lateral scales with light centers from row one up to row 10; some middorsal scales light centered and expanded laterally to form numerous narrow light bands across the dorsum; occasionally, scales between the bands with light centers producing an entirely spotted dorsum; venter often uniformly dark medially, or blotches; intergenials usually 2 + 2 or 2 + 3; hemipenis not greatly expanded laterally or deeply bilobed........................*splendida*
   Basal portion of each dorsal scale light, posterior edge brown, often each scale completely yellow, dorsal bands of completely light scales often apparent; intergenials usually 1 + 2; hemipenis greatly expanded laterally and deeply bilobed........... ....*floridana*

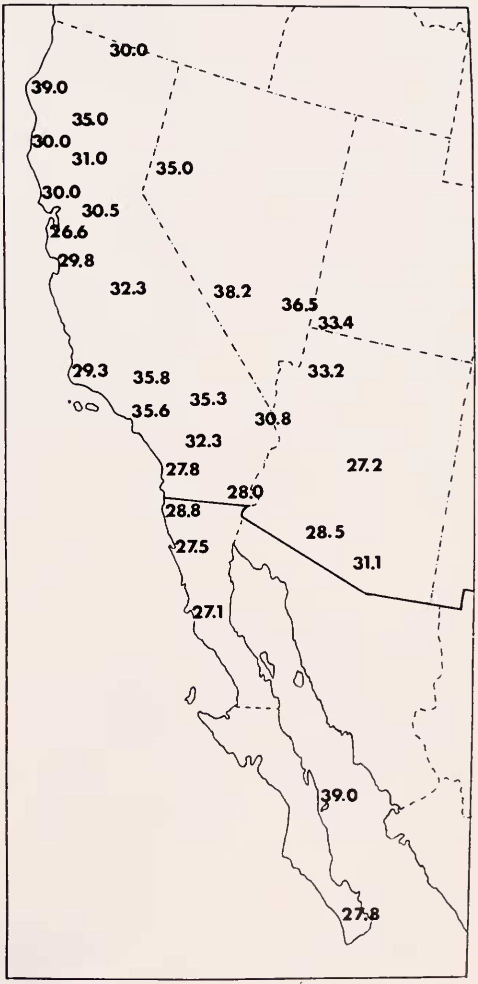
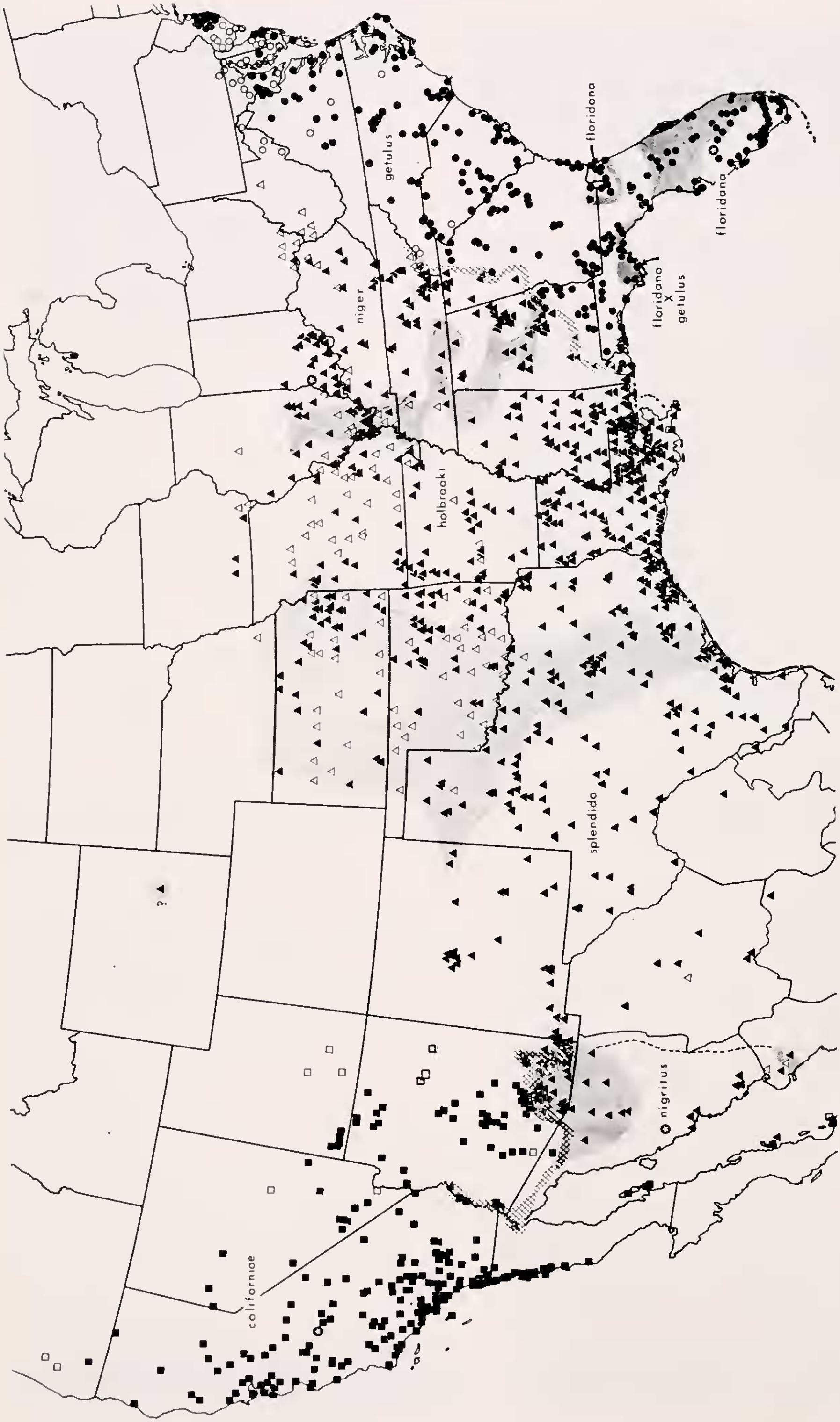


Figure 9. Geographic variation in the number of dorsal body bands in *Lampropeltis getulus* in western United States and Baja California.


getulus
niger
floridana
floridana
floridana x getulus
holbrooki
splendida
nigritus
californiae
?

TAXONOMIC ACCOUNTS
The *getulus* Complex

Lampropeltis getulus getulus (Linnaeus)

Coluber getulus Linnaeus, 1766: 382.
Lampropeltis getulus getulus: Blanchard, 1919: 1.
Lampropeltis getulus sticticeps Barbour and Engels, 1942: 101.
Lampropeltis getulus goini Neill and Allen, 1949: 101.

Holotype.—The data presented for the species apply here.

Definition.—A subspecies of *L. getulus* characterized by 15 to 44 light crossbands on a ground color of chocolate brown to black, a maximum of 21 dorsal scale rows, equal sized genials, 1 + 2 or 2 intergenials, a higher than long or square loreal, and a deeply bilobed and laterally expanded hemipenis.

Range.—Southern half of New Jersey south to northern Florida and west to extreme eastern West Virginia, central Virginia, extreme western North Carolina, the northwestern quarter of Georgia, and southeastern Alabama.

Description.—Ventrals 200 to 223 in males, 201 to 223 in females; subcaudals 45 to 56 in males, 37 to 48 in females; infralabials usually 9 (87.2%), occasionally 10 (11.5%), rarely 8 (1.3%); loreal square (45.5%), slightly higher than long (12.3%), or much higher than long (33.6%), rarely longer or slightly longer than high (6.2% and 1.4%, respectively); intergenials normally 1 + 2 (84.1%) or 2 (11.8%), rarely 1 (2.0%), absent (1.2%), or 2 + 2 (0.9%); anterior genials generally equal to the posterior genials (60.7%), slightly longer (13.3%) or slightly shorter (9.7%), rarely greater (9.7%) or smaller (6.6%); tail length 12.7% (10.9-14.4%) of total length in males, 11.7% (10.1-13.2%) in females; snout length 29.9% (26.8-34.0%) of head length in males, 29.9% (26.7-33.1%) in females.

The color pattern normally consists of white, yellow, or reddish yellow (in young) crossbands on a black, dark brown, or chocolate brown ground color. The bands usually begin on scale row 4 to 8 (patterns 1 and 2, Fig. 13), but in the southern portion of the range, they may extend onto the venter (pattern 3, Fig. 13). These bands often fork anteriorly and posteriorly to connect with adjacent bands (patterns 1 and 2, Fig. 13). The width of the bands varies from half a scale to 10 scales. In general, specimens from the Piedmont in Georgia, North Carolina, Virginia, and Maryland possess narrow bands (pattern 1, Fig. 13) whereas coastal specimens normally have bands 1.5 to 3 scales wide (pattern 2, Fig. 13). Specimens from the Apalachicola region in northern Florida occasionally have unusually wide bands of up to 10 scales (pattern 7, Fig. 13). The ventral pattern is highly variable, ranging from a generally light coloration suffused with dark (especially on the posterior margin of each scute) to a dark coloration with light areas. The juvenile pattern is identical with that of the adult (Fig. 12) except that occasional broods, especially from northern Florida and coastal Georgia, may consist of individuals with reddish yellow bands.

Discussion.—Two populations of *Lampropeltis getulus getulus* are recognizable on the basis of pattern and number of ventrals: a piedmont form with more numerous, narrower bands and a relatively higher number of ventrals, and a coastal form with fewer, wider bands and fewer ventrals. This distinction is valid for populations from New Jersey south to northern Georgia, but in

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← Figure 10. Distribution of *Lampropeltis getulus* in the United States and northern Mexico. Solid symbols represent localities of specimens examined, hollow symbols represent literature records. The *getulus* complex is represented by circles, the *splendida* complex by triangles, and the *californiae* complex by squares. Zones of intergradation within a complex are represented by shading, between subspecies complexes by crosshatching. A small triangle within another symbol represents a locality at which an intergrade between complexes has been found. Type localities are indicated by a star within a circle.

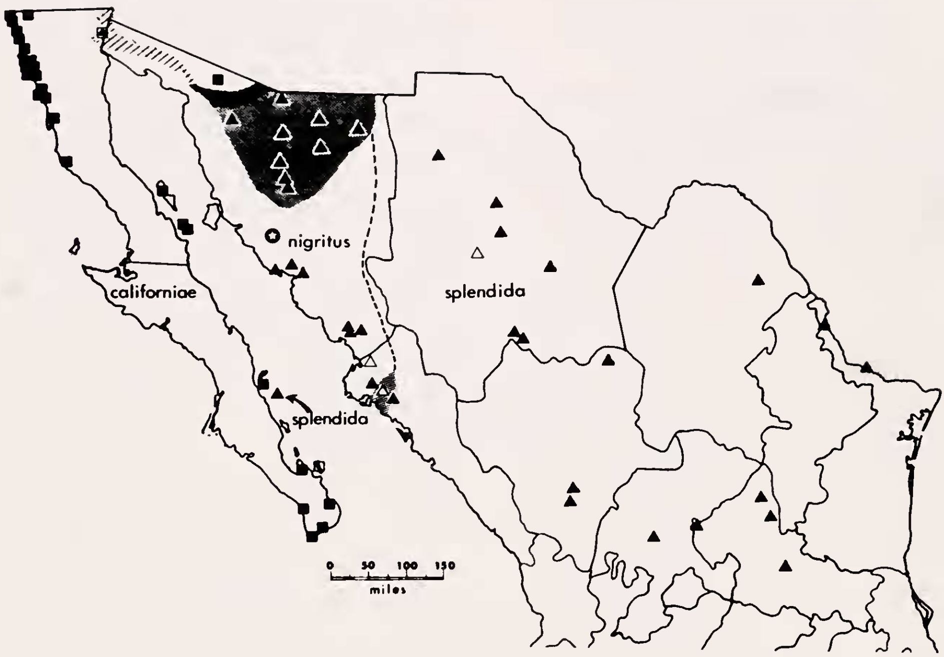


Figure 11. Distribution of *Lampropeltis getulus* in Mexico. For details of interpretation of symbols, see Figure 10.

southern Georgia and Alabama, and northern Florida, the number of ventrals is at the upper limits whereas the pattern is typical of the coastal form. I recognize these two populations as microgeographic races of *L.g. getulus*. Ecological and geographic separation apparently has enabled some degree of differentiation of these two groups, but the degree of differentiation does not warrant their subspecific recognition.

In portions of Florida (especially Wakulla, Leon, Jefferson, Taylor, Dixie and Levy counties) and in coastal Georgia (especially McIntosh County) specimens often possess light spotting between the dorsal bands (pattern 4, Fig. 13). This spotting may coalesce to form distinct bands, especially on the anterior third of the body. In central Florida, especially Alachua and Lake counties, specimens typically have a pattern of 23 to 52 (mean, 36.8) dorsal bands that normally do not fork (pattern 5, Fig. 13). I believe this pattern is the result of addition of bands in the manner described above. This spotting is the result of the influence of *L.g. floridana* as will be discussed below.

Lampropeltis getulus sticticeps Barbour and Engels and *L.g. goini* Neill and Allen are considered intergrades between *L.g. getulus* and *L.g. floridana*, and are discussed under *L.g. floridana*, below.

Lampropeltis getulus floridana Blanchard

Lampropeltis getulus floridana Blanchard, 1919: 1.
Lampropeltis getulus brooksi Barbour, 1919: 2.
Lampropeltis getulus sticticeps Barbour and Engels, 1942: 101.
Lampropeltis getulus goini Neill and Allen, 1949: 101.

Holotype.—USNM 22368 collected by William Palmer at Orange Hammock, DeSoto County (northeast portion), Florida.

Definition.—A subspecies of *L. getulus* characterized by 22 to 66 light crossbands (sometimes obscured) on a chocolate brown ground color that is ontogenetically reduced by basal lightening of each dorsal scale, 23 dorsal scale

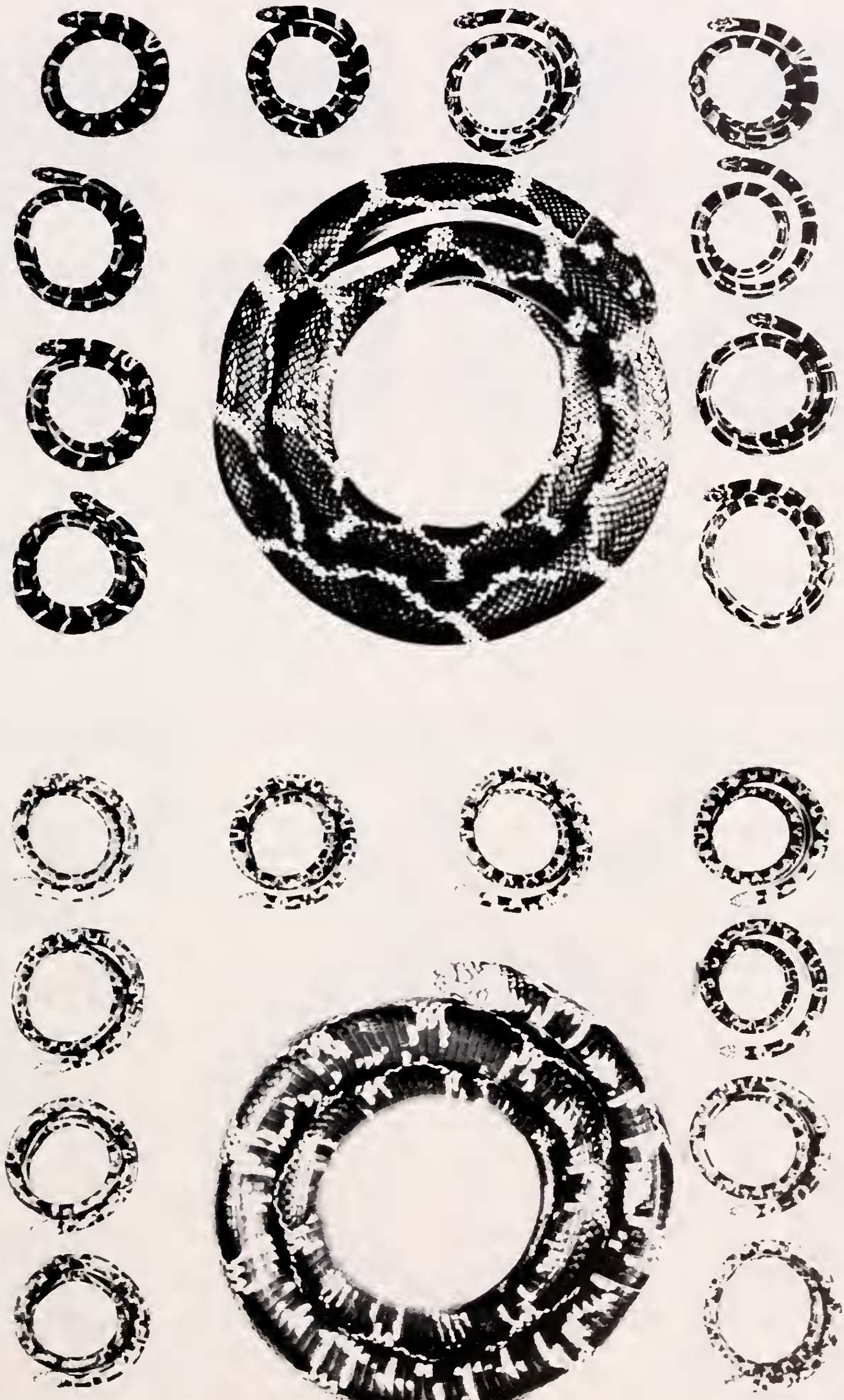


Figure 12. Adult and juvenile patterns of *Lampropeltis getulus getulus,* dorsum above and venter below (NCSM 5789, adult, and 5780-5799, brood, from Minnesota Beach, Pamlico County, North Carolina).

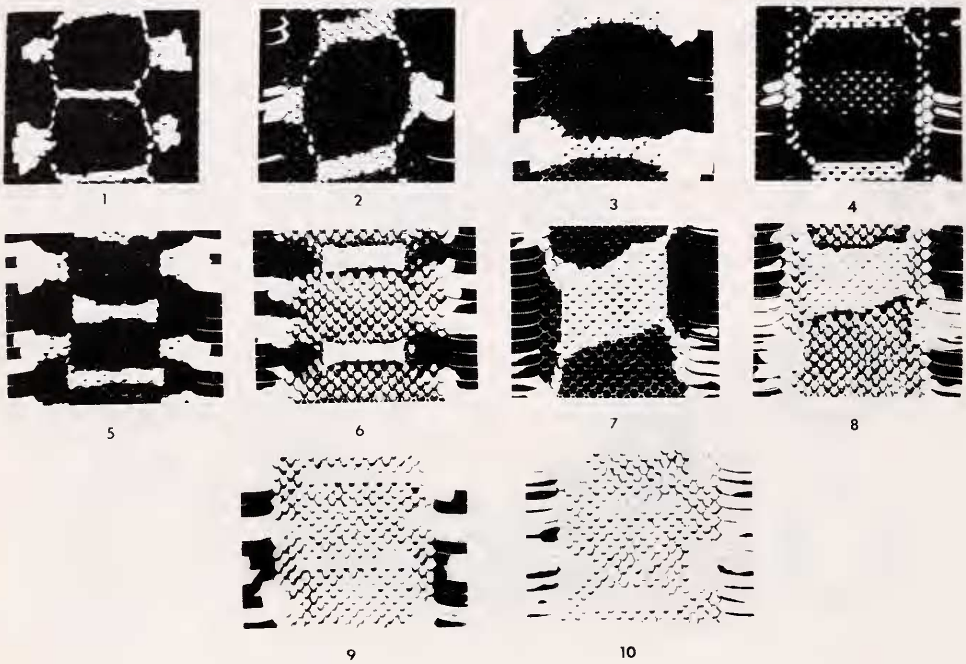


Figure 13. Basic pattern types of the *getulus* complex of *Lampropeltis getulus*. Patterns 1 through 5, *L.g. getulus*; patterns 6 through 8, intergrades between *L.g. getulus* and *L.g. floridana*; patterns 9 and 10, *L.g. floridana*.

rows, equal-sized genials, 1 + 2 or 2 intergenials, a higher than long loreal, and a deeply bilobed and laterally expanded hemipenis.

Range.—Southern Florida as far north as Pinellas and Hillsborough counties on the Gulf coast and southern and western Dade County on the Atlantic coast; a disjunct population in Duval and Baker counties in northeastern Florida.

Description.—Meristic and mensural data for this subspecies are as follows: ventrals 210 to 221 for both sexes; subcaudals 46 to 58 in males, 44 to 55 in females; infralabials usually 9 (85.1%), occasionally 10 (14.9%); loreal usually higher than long (57.9%) or slightly higher (15.8%), occasionally square (21.1%), rarely slightly longer (5.2%); intergenials usually 1 + 2 (86.2%), occasionally 2 (13.8%); anterior genials usually equal in length to the posterior genials (69.0%), occasionally slightly greater (13.8%), greater (6.9%), or smaller (10.3%); tail length 12.8% (10.9-14.3%) of the total length in males, 12.1% (10.2-13.8%) in females; snout length 31.3% (29.6-33.0%) of the head length in males, 30.7% (29.3-32.6%) in females.

The juvenile color pattern normally consists of yellow or reddish yellow crossbands on a brown ground color (Allen and Neill, 1954) (Fig. 14). As the individual matures, the scales in the dark areas between the bands develop light-colored spots on the basal portion of each scale until, in adults, only the posterior tip of each scale remains dark (pattern 9, Fig. 13). The dorsal bands may become almost completely obscured in some individuals (pattern 10, Fig. 13).

Discussion.—The concept of *L.g. floridana* has been severely modified since its original description by Blanchard (1919). Carr (1940), Conant (1958), and Carr and Goin (1959) have considered *L.g. floridana* to have pattern types similar to patterns 5 and 6 (Fig. 13). Their descriptions usually placed emphasis on the number of dorsal bands and light secondary spotting. This modification probably resulted from the recognition of *L.g. brooksi*, which was then distinguished by the differences in pattern. Carr and Goin (1959) characterized *L.g. brooksi* as "dull yellow, the scales being light in color and the dark ground color restricted to a small area on the tip of each scale. The pattern of bands is but slightly or not at all apparent."

Blanchard (1921) stated that *L.g. brooksi* "carries one step farther, and to its logical conclusion the interesting series of pattern changes of the *getulus* group in the southeast," thereby indicating the clinal relationship of the pattern types found from north to south on the Florida peninsula. Duellman and Schwartz (1958) placed *L.g. brooksi* Barbour in the synonymy of *L.g. floridana* Blanchard (which predates *brooksi* by one month) since both pattern types are found in "much of south-central Florida, as well as intermediate individuals over most of the range of *brooksi*." The results of this study support their conclusion.

Examination of the holotype of *L.g. brooksi* (MCZ 12456) revealed that this specimen has a pattern type identical with pattern 10 (Fig. 13). The dorsal bands, although somewhat obscure, are discernible. The pattern of the holotype of *L.g. floridana* is similar to pattern 9 (Fig. 13). The dorsal bands are more obvious as a result of the reduced secondary spotting. Both pattern types are, indeed, found throughout southern Florida and it is apparent that the differences are only a matter of slight degree.

The name *L.g. floridana* should be applied to the southern Florida population which has been considered *L.g. brooksi* by Carr (1940), Conant (1958), and Carr and Goin (1959). The central Florida populations, which typically have

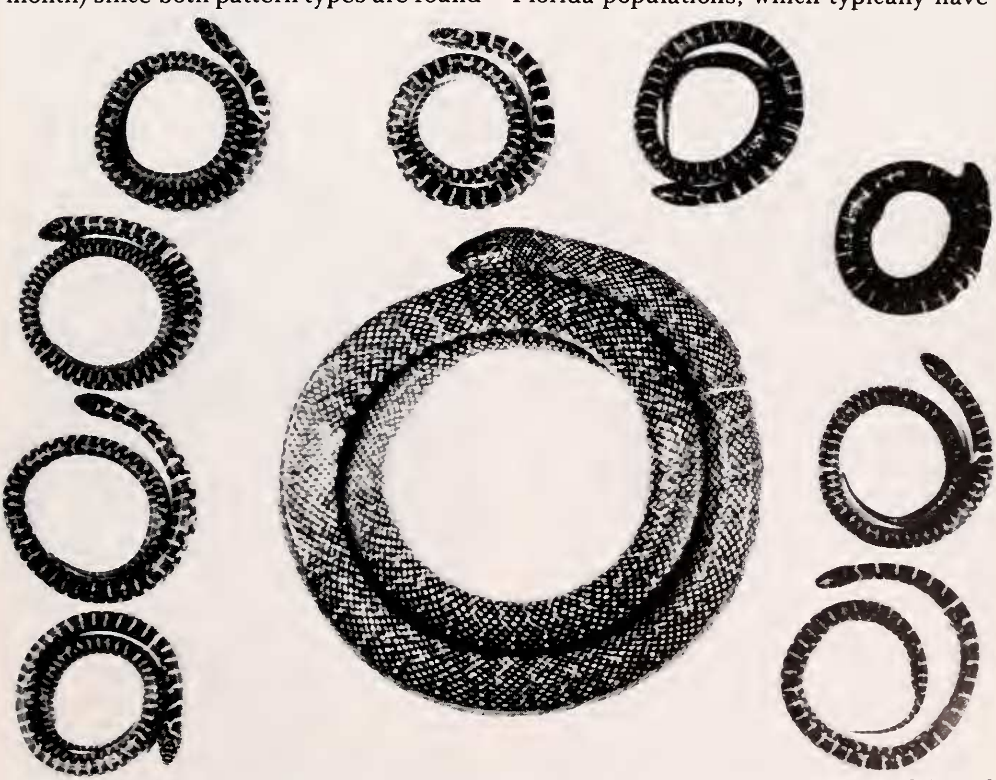


Figure 14. Adult and juvenile pattern of *Lampropeltis getulus floridana* (NCSM 4455, adult, and 4707-4715, brood, from 6 miles S Monroe Station, Monroe County, Florida).

pattern 6 (Fig. 13), should be considered intergrades between *L.g. getulus* and *L.g. floridana*. These populations have been allocated to *L.g. floridana* by the authors noted above. For example, the specimen illustrating *L.g floridana* in the work by Carr and Goin (1959) is actually a specimen of *L.g. getulus* showing slight influence of *L.g. floridana* (pattern 5, Fig. 13).

The pattern of individuals from the zone of intergradation (Fig. 10) varies clinally from pattern 5 in the north with some secondary spotting between the bands (especially anteriorly) to pattern 6 in the south, showing an increase in the degree of secondary spotting. This pattern (6) is found farther south on the eastern coast than on the western coast. Specimens from around Lake Okeechobee (Highlands, Okeechobee, Martin, Palm Beach, Hendry, and Glades counties) are clearly intergrades. Specimens from as far south as Miami along the Miami oölite formation also show this pattern, and I consider them to be intergrades.

The populations of *L. getulus* from the Kissimmee Prairie in southwestern Osceola County, Florida, deserves special mention. This is an intergrade population consisting of individuals with patterns 5, 6, and 9. The area is probably close to the northeastern range limit of the southern Florida *L.g. floridana*.

These intergrade populations are also typically intermediate between *L.g. getulus* and *L.g. floridana* in the character of the number of dorsal scale rows. Fewer specimens possess a maximum of 23 scale rows toward the northern limits of the intergrade zone. However, even among samples of *L.g. getulus* from Alachua County, Florida, about half of the specimens examined possess 23 scale rows. This indicates influence from *L.g. floridana* since it is rare that a specimen of *L.g. getulus* from elsewhere in the range will have 23 dorsal scale rows.

The population of kingsnakes in extreme northeastern Florida (Baker and Duval counties) exhibit all the characters of *L.g. floridana*. Six specimens have been examined from Baker and western Duval counties which possess pattern types 9 or 10 (Fig. 13). For example, UF 2103 from 4 miles E Taylor, Baker County, or UF 3494 (Fig. 15) from between Marxville and Baldwin, Duval County, are indistinguishable from southern Florida populations, except in the number of dorsal bands (23 and 22, respectively, for the two specimens cited, while southern Florida populations average between 53 and 54). Specimens from eastern coastal Duval County and northern St. Johns County are typical *L.g. getulus* X *L.g. floridana* intergrades (pattern 6, Fig. 13), as for example, USNM 14140 from "Pilot town", Duval County, Florida. Since I have not seen any specimens which unquestionably originated from south of this area, I am not certain that the Duval and Baker county population is disjunct, but the evidence provided by intergrade specimens in the southeastern part of this range strongly suggests that this is the case. One specimen, however, USNM 64205 with data given as St. Johns Alligator Farm, St. Augustine, Florida, is allocated to *L.g. floridana*. The low number of dorsal bands (33) indicates that this specimen probably is related to the northeastern population. It is not possible to determine whether this specimen was collected at the Alligator Farm or was collected elsewhere and

Figure 15. ***Lampropeltis getulus floridana*** **(UF 3494 from Duval County, Florida).**

merely sent from the Alligator Farm to be deposited in the National Museum.

Specimens examined from populations immediately north of this apparently disjunct *L.g. floridana* population are primarily *L.g. getulus*. USNM 16698 from Fernandina, Nassau County, Florida, is a typically patterned *L.g. getulus* (pattern 2, Fig. 13) with a maximum of only 21 scale rows (19-21-19). Another specimen (LSUMZ 23509 from Amelia Island, Nassau County, Florida) with the same pattern shows indications of *L.g. floridana* influence in its dorsal scale reduction formula:

$$21 \frac{+6\ (46)}{+6\ (62)}\ 23\ \frac{5\ +\ 6\ (127)}{5\ +\ 6\ (122)}$$

$$21 \frac{4\ +\ 5\ (204)}{4\ +\ 5\ (205)}\ 19\ [218].$$

Specimens from extreme southeastern Georgia are typical *L.g. getulus* with pattern 2 or 3 (Fig. 13). Populations on the offshore islands of McIntosh County, Georgia, however, are variable. UG 994 from Sapelo Island, McIntosh County, Georgia, has pattern 2 and is considered typical *L.g. getulus*, whereas UG 943 has pattern 4, the secondary spotting being most prominent between the anterior bands. In addition, the dorsal scale reduction is as follows:

$$21 \frac{+6\ (38)}{+6\ (49)}\ 23\ \frac{4\ +\ 5\ (96)}{4\ +\ 5\ (105)}$$

$$21 \frac{3\ +\ 4\ (193)}{3\ +\ 4\ (187)}\ 19\ [209].$$

This specimen is therefore considered to be *L.g. getulus* with influence from *L.g. floridana*. Another specimen from the same locality (UG 944) has a pattern more typical of an intergrade (pattern 6, Fig. 13), but has a scale reduction similar to *L.g. getulus*:

$$21 \frac{4\ +\ 5\ (166)}{4\ +\ 5\ (161)}\ 19\ [210].$$

The entire population of Sapelo Island is therefore considered to be *L.g. getulus* with influence from *L.g. floridana*.

A specimen from 10 miles NE Fargo along the Suwannee River, Clinch County, Georgia (UG 400) is a typical intergrade between *L.g. getulus* and *L.g. floridana* (pattern 6, Fig. 13). This locality probably represents the northwestern limit of the zone of intergradation for the northeast Florida *L.g. floridana* population. However, three specimens (USNM 130143-130145) from the Okefenokee Swamp, Charlton Coun-

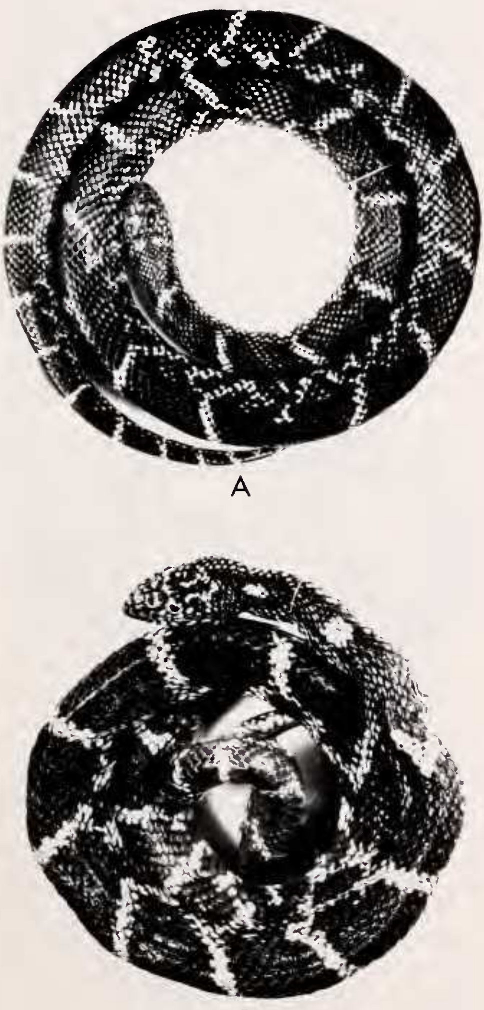


Figure 16. *Lampropeltis getulus* from the Outer Banks of North Carolina showing influence of *L.g. floridana* (A. NCSM 2020 from Hatteras, Dare County, North Carolina; B. MCZ 46469, holotype of *L.g. sticticeps*, from Ocracoke Island, Hyde County, North Carolina).

ty, Georgia, are typical *L.g. getulus*.

Barbour and Engels (1942) described a specimen (MCZ 46469) from Ocracoke Island, Hyde Couty, North Carolina, as a new subspecies, *L.g. sticticeps*, distinguishing it from *L.g. getulus* on the basis of "its broader and flatter head, heavily marked with white" and a pattern in which "the anterior rings appear in the form of spots, and the chain-like pattern does not begin until well down on the body, and from then on the familiar pattern is composed of white bands averaging two and one half to three times as broad as bands in the typical form." They further indicated a behavioral difference "so interesting that this fact alone would warrant its being named... for this snake, unlike all its allies, is not ophiophagous."

There is no question that this specimen is unusual. The head is aberrant in form, and the pattern is unusual for North Carolina. However, I have found spotting between the bands on several specimens from coastal North Carolina (*i.e.*, NCSM 3172 from 11 miles SW Bolton, Columbus County, and NCSM 2020 from Hatteras, Dare County). The holotype of *L.g. sticticeps* and the Hatteras specimen are shown in Fig. 16. There is also a difference in the number of ventral scutes between the specimens from the Outer Banks (200-207, mean 202.7 for 3 males; 204-207, mean 205.7 for 3 females) and the adjacent coastal mainland (206-216, mean 212.4 for 5 males; 205-210, mean 207.3 for 3 females). The Outer Banks population is therefore obviously not derived from the adjacent mainland. It is this difference in ventral count, plus the differences in pattern, head shape and rostrum length that prompted Lazell and Musick (1973) to argue that *L.g. sticticeps* should be considered valid. Their selected data did not consider either individual or geographic variation thereby negating their arguments. I will treat their remarks in detail in a separate paper. On the basis of the color pattern, which is similar to that of *L.g. getulus* X *L.g. floridana* intergrades, I suggest that this population was actually a relict population of *L.g. floridana* (a remnant of the ancestral type that gave rise to *L.g. getulus*) but is now an intergrade population. *L.g. sticticeps* Barbour and Engels should therefore be considered a junior synonym of *L.g. getulus* (Linnaeus) and *L.g. floridana* Blanchard.

Although *Lampropeltis getulus* is often ophiophagous, its diet is by no means restricted to snakes. These kingsnakes will eat any small mammal or bird in addition to reptiles (Clark, 1949; Hamilton and Pollack, 1956; Cunningham, 1959). I have found that individuals may have a preference for one type of prey or another depending on the habitat from which they came. In general, Florida specimens from swamp or marsh habitats tend to be more ophiophagous than specimens from dry areas. For example, several specimens that I collected from a farm near Lamont, Jefferson County, Florida, refused to eat snakes of any size or species, yet readily accepted birds and mammals. The method of killing the prey varied between constriction and the "*Coluber*-like habit" described by Barbour and Engels (1942).

Behavioral characteristics are probably inherited traits, but ones that may be considerably altered by environmental factors. This apparently is the case with the ophiophagous behavior of *L. getulus*. The dietary preferences of individuals may be inherently varied. Depending on the particular habitat, an individual may become habituated to a particular behavior, as for example, a preference for birds and mammals because of their relative abundance.

The kingsnakes in northwestern Florida from Gulf County east to southern Jefferson County differ considerably from neighboring populations. Individuals in that area may have a pattern of 15 to 18 dorsal crossbands, each 4 to 10 scales wide, on a brown ground color (pattern 7, Fig. 13; Fig. 17, C), or may be similarly patterned except that the dorsal scales between the bands are spotted (pattern 8, Fig. 13; Fig. 17, D). Specimens with this pattern formed the basis of the description of *L.g. goini* Neill and Allen (1949). I have, however, also examined specimens from the same population which are typical *L.g. getulus* (Fig. 17, A) or typical *L.g. floridana* (Fig. 17, D). Even specimens from the type locality of *L.g. goini* (Wewahitchka, Gulf County, Florida) may have a pattern more typical of *L.g. getulus* (Fig. 17, B). In addition, several specimens possess a maximum of 23 dorsal scale rows, typical of *L.g. floridana*.

This population, therefore, consists of *L.g. getulus, L.g. floridana*, intermediate specimens, and broad-banded individuals (the significance of which is discussed in the conclusions section below), and is consequently considered to be an intergrade population. The name *L.g. goini* Neill and Allen is therefore placed in the synonymy of *L.g. getulus* (Linnaeus) and *L.g. floridana* Blanchard.

THE *SPLENDIDA* COMPLEX

The *Splendida* Complex
Lampropeltis getulus holbrooki Stejneger

Coronella sayi: Holbrooki, 1842: 99.
Ophibolus getulus sayi: Cope, 1875: 37.
Ophibolus getulus getulus: Cope, 1880: 23.
Lampropeltis holbrooki Stejneger, 1903: 152. Substitute name.
Lampropeltis getulua holbrooki: Bailey, 1905: 47.
Lampropeltis getulus holbrooki: Hurter and Strecker, 1909: 26.
Lampropeltis getulus holbrookii: Strecker, 1909: 7.

Holotype.—None designated. In a footnote, Stejneger (1903) proposed the name *Lampropeltis holbrooki* as a substitute name for Holbrook's (1842) *Coronella sayi*, a misapplication of *Coluber sayi* Schlegel, 1837 (= *Pituophis*

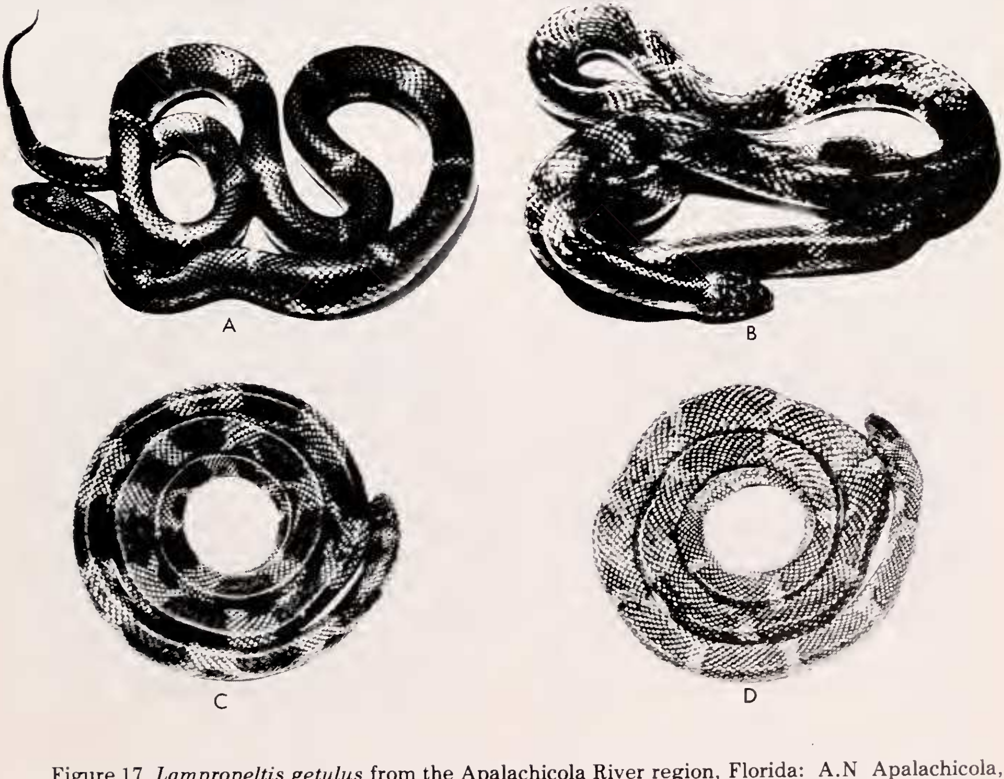


Figure 17. *Lampropeltis getulus* from the Apalachicola River region, Florida: A.N Apalachicola, Gulf County, Florida (specimen not available); B.E. Wewahitchka, Gulf County, Florida (specimen not available); C. LSUMZ 23511 from 6 miles E Wacissa, Jefferson County, Florida; D. LSUMZ 23510 from 3 miles N Carabelle, Franklin County, Florida.

melanoleucus sayi). Stejneger (1903) did not indicate any type locality, but Stejneger and Barbour (1917) gave it as "valley of the Mississippi."

Definition.—A subspecies of *L. getulus* characterized by a dark brown or black ground color with most or all of the dorsal scales having a central light-colored spot, 21 dorsal scale rows, anterior genials equal to or longer than posterior genials, 1 + 2 intergenials, a square loreal, and a slightly bilobed hemipenis.

Range.—Southern Iowa and western Illinois south to eastern Texas, Louisiana, most of Mississippi, and central and southwestern Alabama.

Description.—Ventrals 197 to 221 in males, 198 to 222 in females; subcaudals 46 to 59 in males, 37 to 51 in females; infralabials usually 9 (84.2%), occasionally 10 (14.8%), rarely 8 (0.7%) or 11 (0.3%); loreal square (53.5%), slightly higher than long (12.3%), or slightly longer than high (8.6%), occasionally longer (11.1%) or higher (12.5%); intergenials normally 1 + 2 (83.1%), sometimes 2 + 2 (6.6%) or 2 (7.3%), rarely 2 + 3 (0.3%), 1 (1.3%), or 1 + 1 (1.4%); anterior genials often longer than posterior genials (48.8%), sometimes equal (30.0%), occasionally slightly greater (19.0%), rarely shorter (2.2%); tail length 13.2% (11.0-15.3%) of total length in males, 12.3% (10.1-14.5%) in females; snout length 30.4% (27.7-34.0%) of head length in males, 30.8% (28.4-34.2%) in females.

The pattern of *L.g. holbrooki* includes several different types. In Missouri, western Arkansas, eastern Oklahoma, eastern Texas, and a portion of southwestern Louisiana (excluding the coastal marsh), specimens exhibit pattern 11 (Fig. 22). Each scale of the dorsum has a centrally located, small, round spot. On the first two or three scale rows, however, the spots are larger, leaving only the edges of each scale dark. The ventral pattern may be either uniformly light with the posterior edge of each scute dark, or it may have regular squarish blotches. The ventral side of the tail is light except for the posterior margin of each subcaudal scale. In life the ground color is normally black with pale or bright yellow spotting.

Specimens from the Mississippi River valley from southern Iowa and western Illinois southward to Louisiana possess a very different pattern. The cream or yellow spots in each scale are irregular in shape, and some of the dorsal spots are expanded laterally to form 39 to 94 irregular dorsal bands (pattern 15, Fig. 22). The venter is extremely variable and may range from predominantly light to predominantly dark (Fig. 18). About one-third of the specimens examined from the Louisiana coastal marshes have a red or reddish yellow ventral color.

The pattern found in specimens from eastern Mississippi and western Alabama is more regular than the Mississippi River bottomland type in that the spots are generally symmetrical, although some of the dorsal scales contain spots expanded laterally to form indistinct dorsal bands (pattern 13, Fig. 22).

Intermediate pattern types between the above basic patterns are discussed below.

The juvenile pattern consists of distinct dorsal bands with little or no spotting between the bands, and some spotting on the lateral scale rows (Fig. 19). The spots on the dorsal scales develop with the growth of the individual. Occasional adults have been found which retain the juvenile pattern (Fig. 20, D).

Discussion.—The geographic distribution of pattern types 11, 13, and 15 is shown in Fig. 21. The marked differentiation within *L.g. holbrooki* enables the recognition of three distinct subdivisions that I regard as microgeographic races of *L.g. holbrooki*. Populations intermediate in pattern type have been found between each of these microgeographic races. For example, the Louisiana specimen shown in Fig. 20, A, is typical of the southern populations of the uniformly spotted form (pattern 11), and the kingsnake shown in Fig. 20, C, is typical of the Mississippi bottomland populations (pattern 15). Intermediate specimens (Fig. 20, B) are similar to the spotted form in that the spots are more regular, but some of the spots on the dorsal scales are elongated and oriented laterally forming dorsal bands (pattern 12, Fig. 22). The light spots on the first two or three scale rows are also enlarged so that each scale in these rows may be described as yellow with a dark edge. The kingsnake described by Holbrook (1842) as *Coronella sayi* Schlegel was such an intermediate specimen. Based on his description of pattern, and the number of ventrals and subcaudals, it is probable that Holbrook's specimen from which his figure 22 was drawn, was from

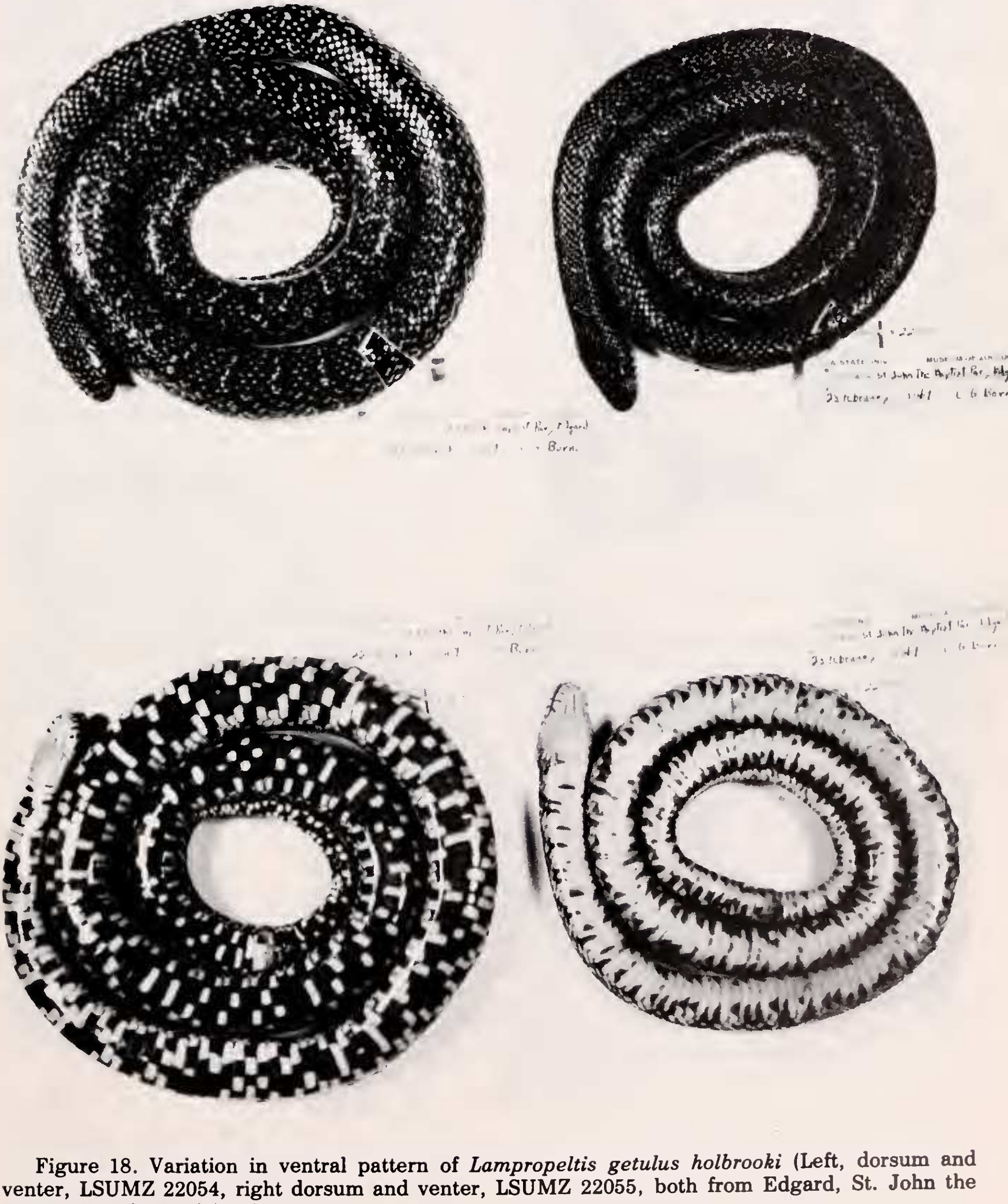
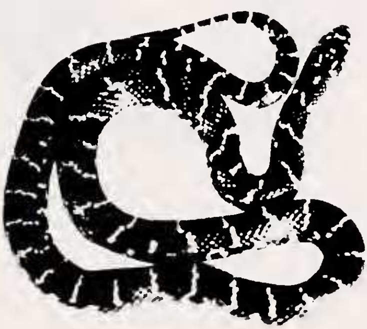


Figure 18. Variation in ventral pattern of *Lampropeltis getulus holbrooki* (Left, dorsum and venter, LSUMZ 22054, right dorsum and venter, LSUMZ 22055, both from Edgard, St. John the Baptist Parish, Louisiana).

A



B

Figure 19. Juveniles of *Lampropeltis getulus holbrooki* (A. LSUMZ 19006 from 0.5 miles NW Kraemer, LaFourche Parish, Louisiana; B. LSUMZ 19336 from Mobile Bay, Baldwin County, Alabama).

central or northeastern Arkansas, certainly not from the Mississippi bottomlands as suggested by Stejneger and Barbour (1917) when they restricted the type locality to the "valley of the Mississippi." The specimen shown by Anderson (1965: 244 B) is also intermediate in pattern, but the *L.g. holbrooki* illustrated by P.W. Smith (1961: 216) is clearly the western form (pattern 11).

Although the three microgeographic races are readily distinguishable, I do not regard their level of differentiation as sufficient to elevate them to subspecific rank. Their degree of differentiation is less than is evident between any other subspecies in the *splendida* complex.

Intergradation between *L.g. holbrooki* and *L.g. niger*, and between *L.g. holbrooki* and *L.g. getulus* is discussed under *L.g. niger*.

Lampropeltis getulus niger (Yarrow)

***Ophibolus getulus niger* Yarrow, 1882: 438.**
***Ophibolus getulus sayi*: Blatchley, 1891: 32.**
***Lampropeltis getulus niger*: Blanchard, 1920: 2.**
***Lampropeltis getulus nigra*: Pratt, 1923: 221.**

Cotypes.—USNM 12149 (2 specimens) collected by Robert Ridgway at Wheatland, Knox County, Indiana.

Definition.—A subspecies of *L. getulus* characterized by a black ground color often with some dorsal scales marked with small light spots to form 21 to 70 dorsal bands, a maximum of 21 dorsal scale rows, anterior genials equal to or longer than posterior genials, 1 + 2 intergenials, a square loreal, and a slightly bilobed hemipenis.

Range.—Eastern Illinois, southern Indiana, extreme central southern Ohio, western West Virginia, Kentucky, eastern two-thirds of Tennessee, northwestern Georgia, and northeastern Alabama.

Description.—Ventrals 198 to 217 in males, 198 to 216 in females; subcaudals 45 to 55 in males, 39 to 51 in females; infralabials usually 9 (82.3%), occasionally 10 (12.3%), rarely 8 (4.6%) or 11 (0.8%); loreal usually square (50.9%), slightly higher than long (11.6%) or higher than long (17.0%), sometimes longer (11.6%) or slightly longer (3.6%); intergenials normally 1 + 2 (78.0%), occasionally 2 (18.1%), rarely 2 + 2 (2.4%) or 1 (1.5%); anterior genials usually equal to posterior genials (42.6%), slightly greater (20.9%) or greater (32.2%), rarely shorter (4.3%); tail length 13.0% (10.8-14.6%) of total length in males, 12.2% (10.0-13.7%) in females; snout length 30.2% (27.0-32.3%) of head length in males, 31.1% (29.4-33.6%) in females.

The dorsal pattern is essentially a reduced juvenile pattern of *L.g. holbrooki*. Juvenile *L.g. niger* (Fig. 23) have a pattern similar to *L.g. holbrooki*, but usually with fewer bands. As the individual matures, this pattern becomes reduced. The adult pattern may retain the dorsal bands only as a series of spots (pattern 17, Fig. 22), or they may be so reduced as to be almost indiscernible (pattern 18, Fig. 22).

Discussion.—Blanchard (1921) recognized that the pattern of *L.g. niger* is simply a reduction of the *L.g. holbrooki* juvenile pattern. He believed *L.g. niger* to be a valid subspecies, but indicated the possibility that it might be only a "local or inconsistent variation of *holbrooki.*" The results of my study confirm that *L.g. niger* is a valid subspecies readily identified by its pattern. Although occasional specimens of *L.g. holbrooki* may be similar in pattern to *L.g. niger* through retention of the juvenile pattern (Fig. 20, D), no specimens were found within the defined range of *L.g. niger* that had developed secondary spotting similar to that of *L.g. holbrooki* (Fig. 24). Specimens from the periphery of the range, however, develop spotting laterally and dorsally and are considered intergrades between *L.g. niger* and *L.g. holbrooki* (pattern 16, Fig. 22).

P.W. Smith (1961) stated that intergradation between *L.g. holbrooki* and *L.g. niger* in Illinois "is exhibited by specimens from extreme southwestern Illinois, and intergrades probably occur in most of the southern Division." Specimens from Coles, Cumberland, Jasper, and Richland counties, Illinois, are typical *L.g. niger* whereas Shelby and Effingham county specimens have pattern 16 (Fig. 22) and are considered intergrades. A specimen (UIMNH 50818) from 4 miles SE Carlinville, McCoupin County, Illinois, is intermediate between patterns 12 and 16, and is considered *L.g. holbrooki* with *L.g. niger* influence. This probably represents the northwestern limit of the zone of intergradation. However, another specimen (INHS 3031) from 4 miles N Old Ripley, Bond County,

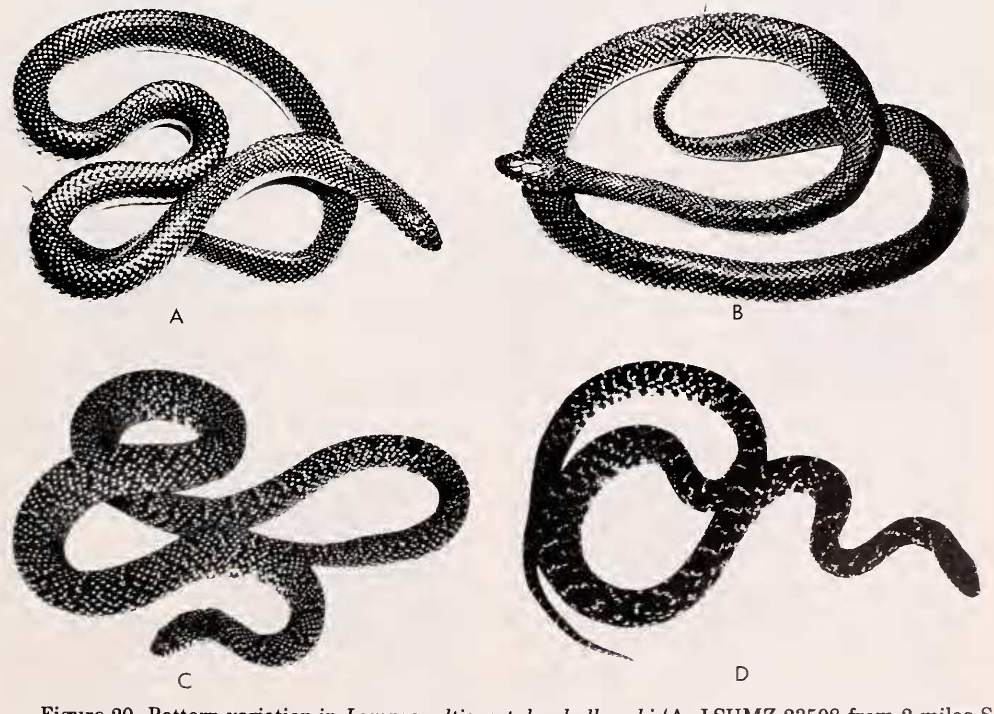


Figure 20. Pattern variation in *Lampropeltis getulus holbrooki* (A. LSUMZ 23508 from 2 miles S Holmwood, Calcasieu Parish, Louisiana; B. RAT uncatalogued specimen from Lafayette, Lafayette Parish, Louisiana; C. and D. LSUMZ 19004 and 19007 from 0.5 miles NW Kraemer, LaFourche Parish, Louisiana).

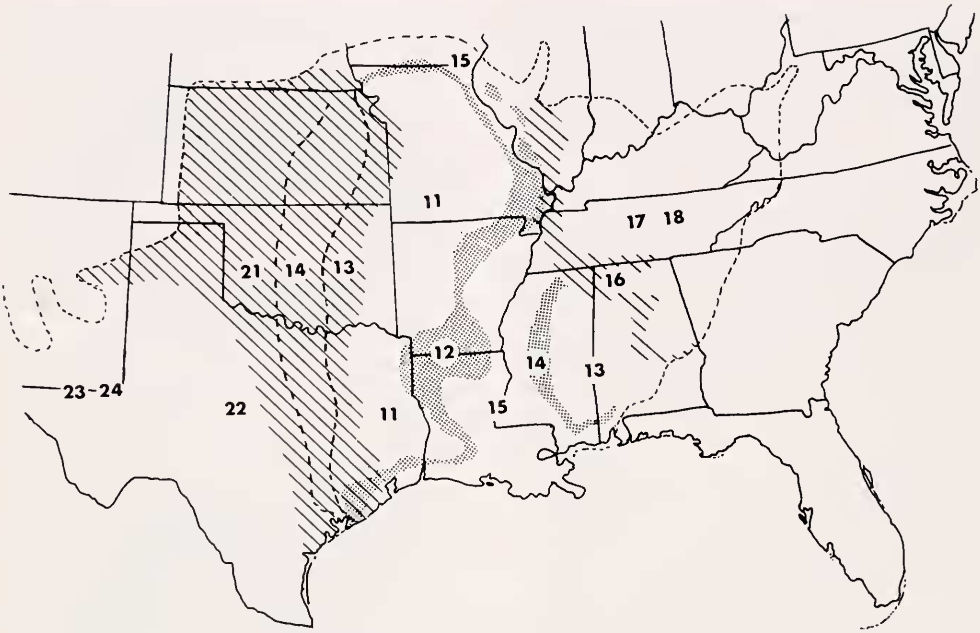


Figure 21. The geographic distribution of pattern types in the *splendida* complex of *Lampropeltis getulus*. Numbers refer to pattern types in Figures 22 and 31.

Illinois, (southeast of the McCoupin County record) is typical of *L.g. holbrooki* (pattern 11). The entire population in southern Illinois (southeast of Randolph County), extreme western Kentucky (Trigg County westward), and northwestern Tennessee consists of intergrades. The specimen labled *L.g. niger* by P.W. Smith (1961: 217) is an intergrade between *L.g. niger* and *L.g. holbrooki.*

Specimens from southern Tennessee from Franklin County westward are also intergrades between *L.g. niger* and *L.g. holbrooki.* MSU 1545 from 2 miles NW Myrtle, Union County, Mississippi, has a reduced *L.g. holbrooki* pattern with very small spots between the dorsal bands and small lateral spots, thereby showing influence of *L.g. niger*. This locality marks the northeastern limit of *L.g. holbrooki* in Mississippi. The zone of intergradation in central Alabama is evidenced by intermediate specimens (pattern 16, Fig. 22) from St. Clair, Jefferson, Shelby, Chilton, and Elmore counties. The insufficient number of specimens from northern Alabama does not permit an accurate analysis of the zone of intergradation in this area. Two specimens from Colbert County (USNM 51217 from Leighton and USNM 2319 from Tuscumbia), however, are typical of *L.g. niger*. USNM 51217 shows a slight tendency toward pattern 16. A specimen (UAHC 52-1077) from Smither's Mountain, near Huntsville, Madison County, is clearly an intergrade (Fig. 25).

Relationships with The *Getulus* Complex

Typical adult *L.g. niger* may have a completely dark dorsum with only slight traces of the juvenile crossbands, which are represented by a series of light spots (Fig. 24, A and B). The degree of ontogenetic pattern reduction varies individually, not geographically. Adult specimens often retain distinct dorsal bands (Fig. 24, C). Occasional adult specimens may retain the broad juvenile bands, as for example, LSUMZ 19015 (Fig. 24, D), a male with a total length of 1100 mm. Such specimens are distinguished from *L.g. getulus* by the bands, which are always composed of a series of

Figure 23. Juvenile pattern of *Lampropeltis getulus niger* (from 12.5 air miles SSE Benton, Polk County, Tennessee; specimen not available).

spots rather than continuous as in the latter form.

Blanchard (1921) emphasized the number of dorsal bands as a criterion in distinguishing *L.g. niger* from *L.g. getulus*. He cited a specimen of *L.g. getulus* from the Cherokee Nation, North Carolina (USNM 15291), with 37 cross-bands (30 on the body) which "presents a strong contrast with one [*L.g. niger*] from *getulus*, but their number is 38 and 31 [body + tail bands], respectively, and one would doubtless not hesitate to assign them to *getulus*." The Augusta specimen (USNM 8797) is a female *L.g. niger* (pattern 17) with only 24 dorsal bands and 209 ventrals. The reduced number of bands results from loss of bands by extreme darkening. However, all other specimens from this area to northeastern Georgia are typical of *L.g. getulus*. Furthermore, the number of ventrals is a little low for this area (mean 215.1, range 210 to 220, for females). The locality data, therefore, are doubtful. USNM 9109 from Marietta, Cobb County,

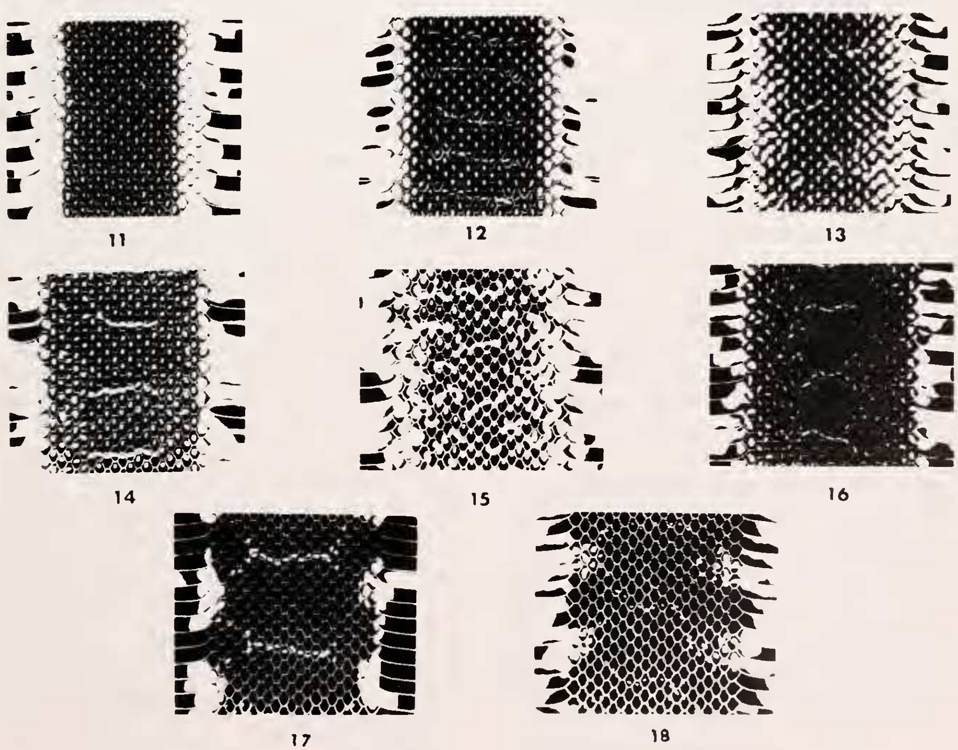


Figure 22. Basic pattern types of the eastern representatives of the *splendida* complex of *Lampropeltis getulus*. Patterns 11 through 15, *L.g. holbrooki*; pattern 16, intergrade between *L.g. holbrooki* and *L.g. niger*; pattern 17 and 18, *L.g. niger*.

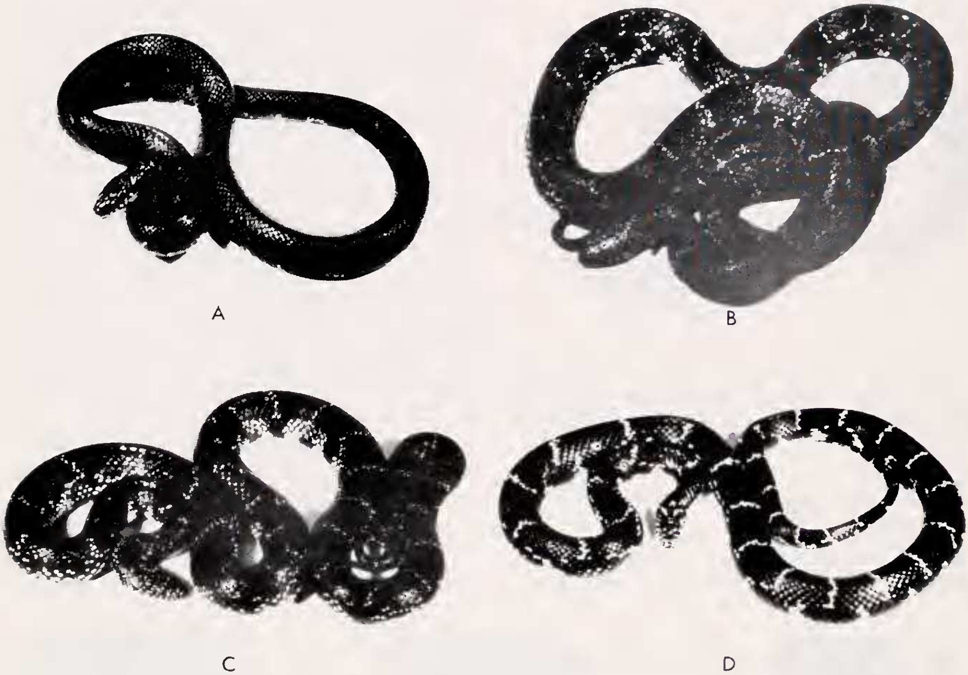


Figure 24. Pattern variation in *Lampropeltis getulus niger* (A. and B. LSUMZ 19027 and 19028 from the Chatahoochee National Forest, 14 air miles NNE Chatsworth, Murray County, Georgia; C. LSUMZ 19012 from Dentville, McMinn County, Tennessee; D. LSUMZ 19015 from the Cherokee National Forest, 12.5 miles SSE Benton, Polk County, Tennessee).

so short a distance west as Knoxville, Tennessee, with 73." I have found a great amount of variation in dorsal band number in *L.g. niger*. In eastern Tennessee, for example, the average number of body bands, when present, is 40.1, but the number varies from 21 to 61.

Blanchard (1921) further stated that *L.g. getulus* and *L.g. niger* "might be supposed to be distinct even where their ranges meet, but specimens from Georgia and Alabama practically prove intergradation. The specimens from Marietta and from Augusta, Georgia, cited by Yarrow (1882: 91), have the cross bands very narrow, unlike any typical Georgia, is also typical *L.g. niger* (pattern 17). This female has 30 dorsal bands and 203 ventrals which is within the limits of the *L.g. niger* populations in northwestern Georgia. Another specimen (UIMNH 18625), a male from 4 miles S Hapeville, Clayton County, Georgia, is typical of *L.g. getulus* (pattern 1) with 21 dorsal bands and 215 ventrals. Data for this animal agree with adjacent *L.g. getulus* populations. The distance between these two localities is only about 20 miles.

A third specimen (UIMNH 35739), a male from Atlanta, Fulton County, midway between the above two localities, is intermediate in pattern (pattern 19, Fig. 26) and has 207 ventrals and 19 dorsal bands. I consider this specimen to be an intergrade between *L.g. getulus* and *L.g. niger*.

The occurrence of intergradation between members of the *splendida* complex (both *L.g. niger* and *L.g. holbrooki*) and *L.g. getulus* is rare. In addition to the above mentioned specimen, I have seen intergrades between *L.g. niger* and *L.g. getulus* in Lee County, Alabama. King (1939) reported another specimen (unavailable) from Deals Gap at the southwestern end of the Great Smoky Mountains National Park as "a perfect intergrade between *L.g. getulus* and *L.g. nigra*."

In Lee County, Alabama, *L.g. niger* and *L.g. getulus* are sympatric at least from 10 miles south to 9 miles north of Auburn, and west to Loachapoka. The two subspecies are again readily distinguishable on the basis of pattern with the bands of *L.g. niger* consisting of a series of spots and the bands of *L.g. getulus* being continuous (Fig. 27). Specimens of *L.g. getulus* also tend to have a higher number of ventrals: 215 (210-220) for *getulus*, 212.2 (210-216) for *niger*, and 210.7 (207-212) for intermediates. In this area, *L.g. getulus* is apparently the common form, since 8 of the 16 specimens examined (AU collections) are of this subspecies, 4 are *L.g. niger*, and 4 are intermediate. I do not know whether there is ecological separation in this area. AU 34 from Dowdells Swamp, 10 miles SW Auburn, is typical of *L.g. niger* (pattern 17), while AU 890 with locality data given only as 10 miles SW Auburn, is typical of *L.g. getulus* (pattern 1). AU 429 from 10 miles SW Auburn is intermediate (Fig. 28).

In addition to the pattern, the distinctiveness of the hemipenial form is diagnostic. Members of the *getulus* complex have hemipenes that are expanded at the distal end, while the hemipenes in the *splendida* complex are not expanded. The everted hemipenes of all of the intergrade specimens are intermediate in hemipenial form (Fig. 29).

Available specimens intermediate between *L.g. holbrooki* and *L.g. getulus* are equally rare: AU 9118 from 3.9 miles S Georgiana, Butler County, Alabama; AU 6246 from Holy Mill Creek, 3 miles W Blacksher, Baldwin County, Alabama; AU 8859 from Perkins Landing on the Tensaw River, 8.6 air miles WSW Bay Minette, Baldwin County, Alabama; AU 8996 from the Baldwin—Mobile County line, Mobile Bay Causeway (US 90). The pattern of *L.g. getulus* and *L.g. holbrooki* intergrades consists of wide, distinct bands across the central 8 to 12 scale rows with some secondary spotting between the bands and on the lateral

Figure 25. Intergrade between *Lampropeltis getulus holbrooki* and *L.g. niger* (UAHC 52-1077 from Smither's Mountain, Madison County, Alabama).

scales (pattern 20, Fig. 26). The hemipenis of one of the two males is everted and is also intermediate in form (Fig. 29).

Another Monroe County specimen (AU 2964) from Hybart (9 miles N Holly Mill Creek) is typical of *L.g. holbrooki* with 45 dorsal bands (compared with 27 for AU 6246) and 218 ventrals (compared to 208 for AU 6246, both females).

Additional locality records for Baldwin County are as follows: *L.g. getulus*—Silver Hill (MCZ 47885); 3 miles S US 31 on Alabama 112, east of Bay Minette (Yancy Junior College, Bay Minette, uncatalogued specimen); Midway on Morgan Peninsula (AU 3830); *L.g. holbrooki*—0.8 miles E Apalachee River, US 90, Mobile Bay (LSUMZ 19336); 1.0 mile E Apalachee River, US 90, Mobile Bay (LSUMZ 19010).

The distribution of *L.g. getulus, L.g. niger,* and *L.g. holbrooki* strongly indicates that there is a narrow zone of contact between *L.g. getulus* and *L.g. niger*, and *L.g. getulus* and *L.g. holbrooki*, with only occasional interbreeding. This phenomenon suggests that *L.g. getulus* is not derived from either *L.g. niger* or *L.g. holbrooki*.

Lampropeltis getulus splendida (Baird and Girard)

Ophibolus splendida Baird and Girard, 1853: 83.
Ophibolus sayi: Baird and Girard, 1853: 159.
Ophibolus getulus splendidus: Cope, 1875: 37.
Ophibolus getulus sayi: Brown, 1901: 77.
Lampropeltis getulus splendidus: Wright and Bishop, 1915: 148.
Lampropeltis getulus splendida: Blanchard, 1920: 2.
Lampropeltis catalinensis Van Denburgh and Slevin, 1921: 397.
Lampropeltis getulus catalinensis: Soule and Sloan, 1966: 142.

Holotype.—USNM 1726 collected by Col. J.D. Graham in Sonora, Mexico.

Definition.—A subspecies of *L. getulus* characterized by a dark brown or black ground color with each of the lateral scales having a central light-colored spot and occasional light scales in the medial scale rows forming 42 to 97 crossbands, 23 or 25 dorsal scale rows, anterior genials usually much longer than posterior genials, usually 2 + 2 intergenials, a square or longer than high loreal, and a moderately bilobed hemipenis.

Range.—Central Texas west to southeastern Arizona and southward to San Luis Potosi and Zacatecas, Mexico, and Santa Catalina Island, Gulf of California, Mexico.

Description.—Ventrals 199 to 227 in males, 203 to 237 in females; subcaudals 45 to 62 in males, 40 to 52 in females; infralabials usually 9 (83.0%), occasionally 10 (17.0%); loreal square (38.4%), slightly longer than high (22.6%) or longer than high (22.1%), rarely higher than long (9.5%) or slightly higher than long (7.4%); intergenials normally 2 + 2 (62.0%), often 2 + 3 (22.2%) especially in the western portion of the range, occasionally 1 + 2 (10.9%) in the eastern part of the range, rarely 2 (4.6%) or 1 + 1 (1.0%); anterior genials usually much longer than the posterior genials (62.8%), or slightly longer (21.0%), occasionally equal (16.2%); tail length

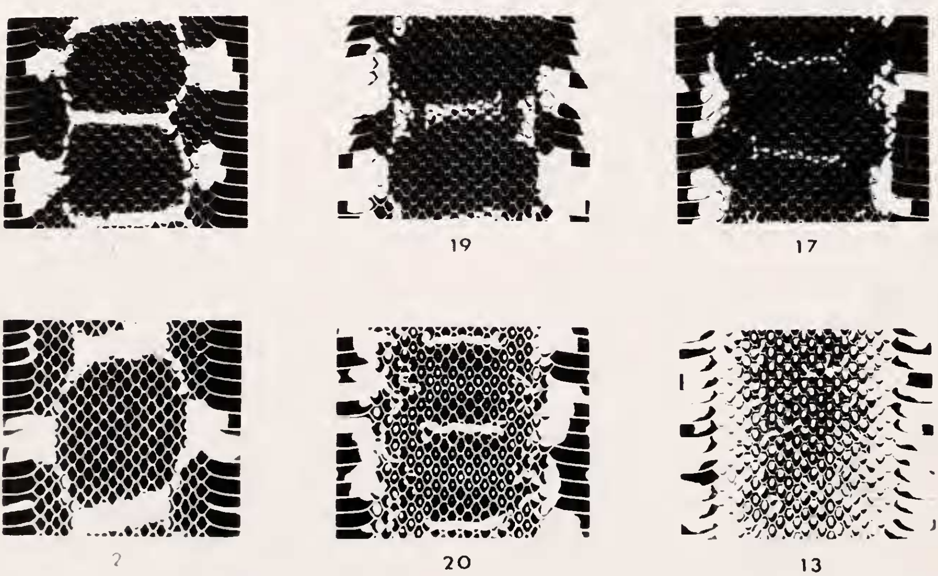


Figure 26. Pattern types of intergrades between *Lampropeltis g. getulus* and the eastern members of the *splendida* complex (*L.g. holbrooki* and *L.g. niger*). Patterns 1 and 2, *L.g. getulus*; pattern 19, intergrade between *L.g. getulus* and *L.g. niger*; pattern 20, intergrade between *L.g. getulus* and *L.g. holbrooki*; pattern 17, *L.g. niger*; pattern 13, *L.g. holbrooki.*

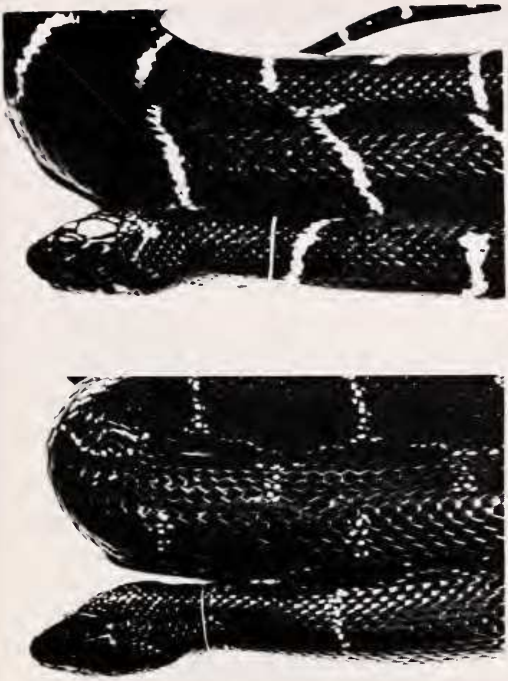


Figure 27. Specimens from the area of sympatry for *Lampropeltis g. getulus* and *L.g. niger* (Top, *L.g. getulus*, AU 416 from 5 miles S Auburn, Lee County, Alabama; bottom, *L.g. niger*, AU 35, from 4.5 miles NW Loachipoka, Lee County, Alabama).

13.4% (10.9-14.1%) of total length in males, 12.4% (11.3-13.5%) in females; snout length 30.5% (27.9-32.2%) of head length in males, 31.2% (29.4-33.2%) in females.

The pattern usually is as illustrated in Fig. 31, pattern 23, with yellow or cream spotting. The venter is usually dark except for the light anal plate. Dorsal bands may consist of a series of spots, may be broad (to two scales wide), or may be absent. Occasional specimens may be completely spotted with the dorsal scales each containing a centrally located light-colored spot, although these spots are usually smaller than the lateral spots (pattern 24, Fig. 31). Specimens from the eastern limits of the range often have an irregular pattern with a blotched rather than a uniform venter (pattern 22, Fig. 31). Juvenile patterns do not differ from that of the adult.

Discussion.—Van Denburgh and Sleven (1921) described *Lampropeltis catalinensis* from Santa Catalina Island, Gulf of California, on the basis of a single adult male (CAS 50514) "which was dug out from the center of a decayed fallen cactus" (Van Denburgh, 1922). Van Denburgh and Slevin (1921) described the pattern as follows: "no transverse markings, a dark purplish brown longitudinal dorsal band about five scales wide from head to end of tail. All lateral scales yellowish white with narrow purplish brown borders. Along the middorsal line, at nearly regular intervals of three or four scales, are small yellowish white spots on single scales. Head dark brown above and laterally, with small yellowish white markings on internasals, prefrontals, temporals, oculars, loreal, nasals, rostral, and labials. Lower surfaces chiefly black, marbled with yellowish

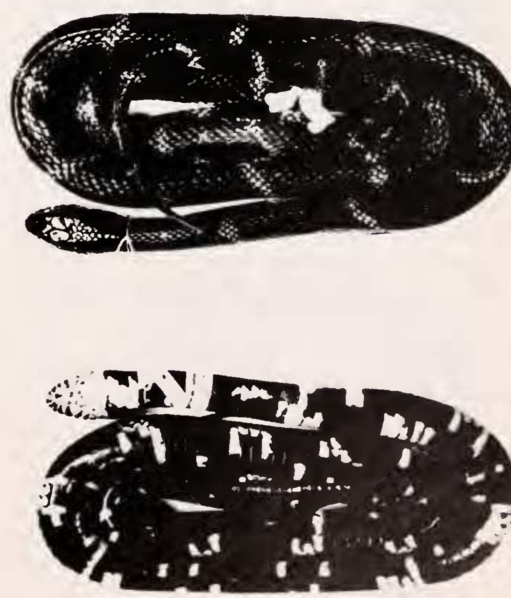


Figure 28. An intergrade between *Lampropeltis g. getulus* and *L.g. niger* (dorsum and venter of AU 429 from 10 miles SW Auburn, Lee County, Alabama).

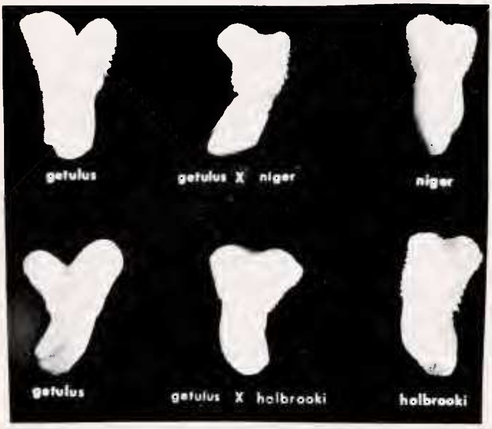


Figure 29. Hemipenes of intergrades between members of the *getulus* complex and the *splendida* complex of *Lampropeltis getulus*. Top row—*L.g. getulus*, NCSM 5175 from 4¾ miles NW Laurel Hill, Scotland County, North Carolina;*L.g. getulus* X *L.g. niger*, AU 429 from 10 miles SW Auburn, Lee County, Alabama; *L.g. niger*, UF 10775 from Euchee Focks, Meigs County, Tennessee. Bottom row—*L.g. getulus*, UF 2998 from 4 miles E Thomasville, Thomas County, Georgia; *L.g. getulus* X *L.g. holbrooki*, AU 9159 from 1.5 air miles W Bleckshер, Baldwin County, Alabama; *L.g. holbrooki*, MSU 1639 from the west end of Horn Island, Jackson County, Mississippi.

white laterally on most of the gastrosteges, and centrally on a few; the distal urosteges and the genials and gulars yellowish white with black or brown margins." Van Denburgh (1922) added that "the ground color above is dark purplish brown, similar to that of some specimens of *L. californiae*." This purplish brown coloration is the same as the chocolate brown that I have used to describe the lighter colored specimens. Van Denburgh (1922) further stated that the coloration "is quite different from any other known species, although the lower surfaces are somewhat suggestive of *L. nitida* and the spotted sides remind one of *L.g. splendida*."

Cliff (1954) shortened the description of the coloration to "a purple longitudinal dorsal band..." and stated that "the only other *Lampropeltis* with a color pattern near that of *catalinensis* is *L. nitida* from the Cape region of Baja, California."

The following data were obtained from the holotype (CAS 50514): ventrals 226; subcaudals 62; supralabials 8, fourth and fifth entering the orbit; infralabials 10/9; temporals 2 + 4/2 + 3; oculars 1 + 2; anterior genials much longer than posterior; intergenials 2 + 3; dorsal scale reduction

$$23 \ \frac{4 + 5\ (147)}{6 + 7\ (138)} \ 21 \ \frac{3 + 4\ (183)}{3 + 4\ (190)} \ 19;$$

length 984 + 157 mm; pattern type 23 with 68 narrow crossbands consisting of a series of light spots.

The pattern of *L. catalinensis* is identical in all respects with that typical of *L.g. splendida* (Fig. 30). In addition, the holotype of *L. catalinensis* agrees in all other characters with *L.g. splendida* except in the number of supralabials. Only 4.4% of the specimens examined possess 8 supralabials. Allowing, however, for individual variation in this character, *L. catalinensis* Van Denburgh and Slevin is identical with and therefore should be considered a synonym of *L.g. splendida* (Baird and Girard).

L.g. splendida intergrades over a broad geographic area with *L.g. holbrooki* (Fig. 10). Specimens from the eastern portion of the range of *L.g. splendida* tend to have a pattern of irregular crossbands and a blotched venter (pattern 22, Fig. 31). Farther east, the pattern becomes intermediate as the scales between the dorsal bands develop spotting (pattern 21, Fig. 31) until the pattern becomes more like *L.g. holbrooki.* The influence of *L.g. splendida* on the *L.g. holbrooki* pattern 11 is apparent in the formation of dorsal bands (similar to pattern 13) which become more prominent in specimens from farther west (similar to patterns 14 and 15). Since specimens from this eastern part of the intergrade zone appear similar to *L.g. holbrooki* in pattern, populations in Kansas and Oklahoma have been identified as *L.g. holbrooki.* Webb (1970) stated that "characteristics applicable to *splendida* have been noted in some individuals of *holbrooki.* Five of 71 Oklahoma specimens have 23 scale rows at midbody (*splendida*) but some *holbrooki* have 23 instead of 21 scale rows (Blanchard, 1921: 25, 34, 105)." He further stated that the two subspecies "may intergrade in southwestern Oklahoma." H.M. Smith (1956) stated that specimens of *L.g. holbrooki* from southwestern Kansas approach *L.g. splendida* in color pattern, but in other respects are typical of *L.g. holbrooki*. Nonetheless, neither author recognized an intergrade zone in their respective states.

Blanchard's (1921) statements that *L.g. holbrooki* sometimes has 23 dorsal scale rows were based on specimens from the intergrade zone described above. Specimens from this zone in Kansas, Oklahoma, and central Texas may have either 21 or 23 dorsal scale rows. In addition, the number of intergenials may be either 1 + 2 (59.4%) or 2 + 2 (35.5%). This is intermediate between *L.g. holbrooki* (83.1% have 1 + 2, only 6.6% with 2 + 2) and *L.g. splendida* (62.0% have 2 + 2, only 10.2% with 1 + 2). As would be expected in an intergrade zone, occasional specimens appear to have the pattern of either one form or the other. KU 16920 from 8 miles NE Clay Center, Clay County, Kansas, has pattern 23 (*L.g. splendida*), with the anterior part of the body intermediate between pattern 21 and 23 (influence from *L.g. holbrooki*). UMMZ 72357 from Osborne County, Kansas, has a pattern typical of *L.g. splendida* (pattern 23) except that the venter is blotched. This specimen also has only 21 dorsal scale

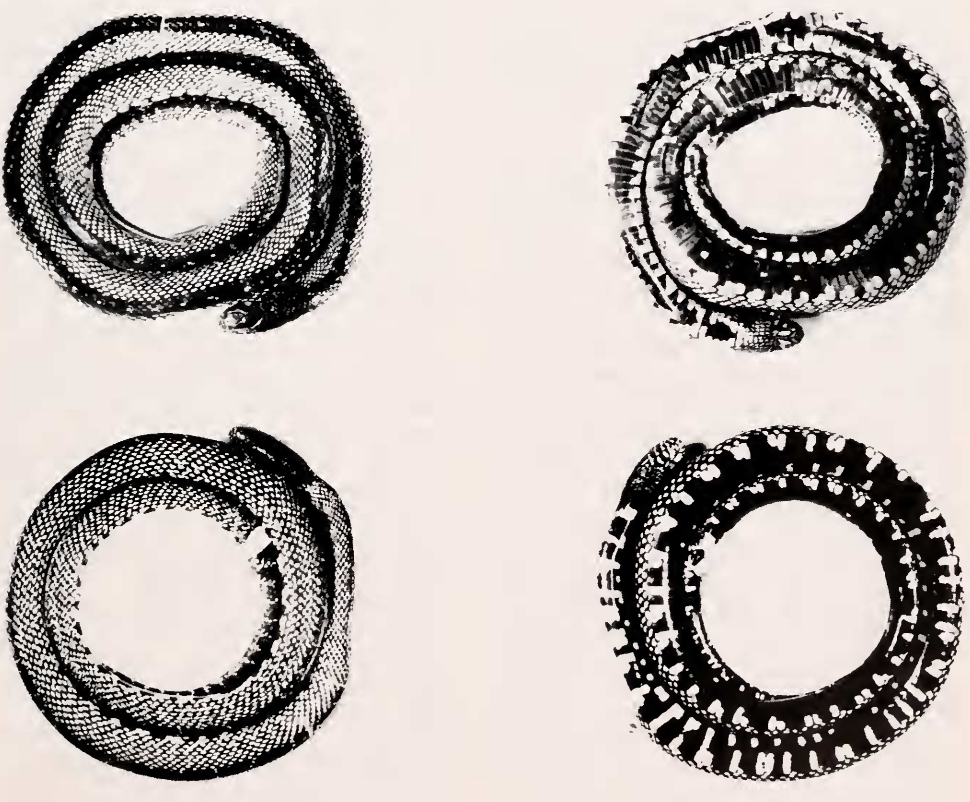


Figure 30. *Lampropeltis getulus splendida*. Top row dorsum and venter of CAS 50514, the holotype of *L. catalinensis*, from Santa Catalina Island, Gulf of California, Mexico; bottom row, dorsum and venter of LACM 3215 from 2 miles W Las Cruces, Dona Ana County, New Mexico.

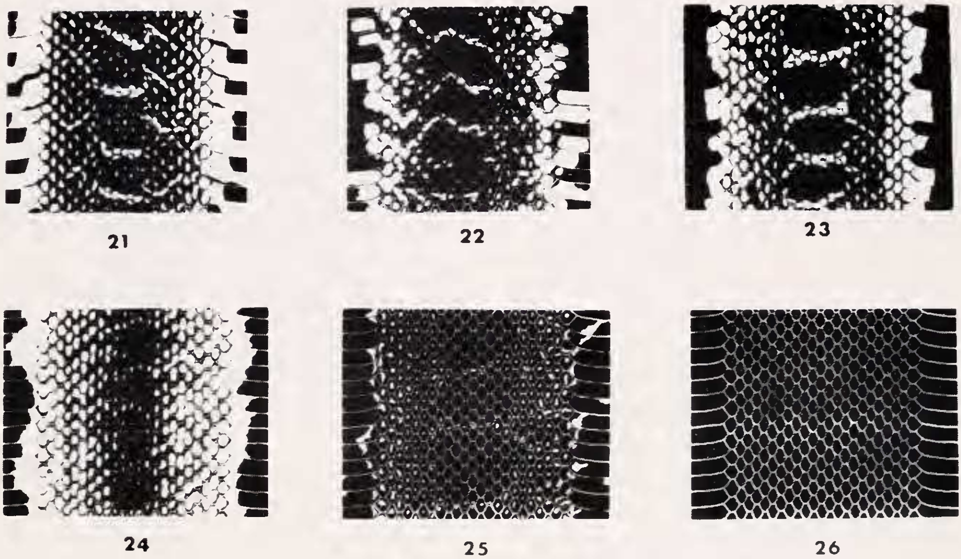


Figure 31. Basic pattern types of the western representatives of the *splendida* complex of *Lampropeltis getulus*. Pattern 21, intergrade between *L.g. splendida* and *L.g. holbrooki*; patterns 22 through 24, *L.g. splendida*; patterns 25 and 26, *L.g. nigritus*.

rows and 1 + 2 intergenials. This is also the case for UIMNH 18271 from 2 miles E Kearney County, Kansas. A specimen (UMMZ 126340), from 2.5 miles S Springer, Carter County, Oklahoma has a pattern intermediate between 21 and 23. One specimen (OSU R-161) from 4 miles N and 2 miles E Stillwater, Payne County, Oklahoma, is typical of *L.g. holbrooki* (pattern 11) but all other specimens from this area either show influence of *L.g. splendida* (pattern between 21 and 11), as, for example, OSU R-273 from Stillwater, Payne County, or show equal influence of both *L.g. splendida* and *L.g. holbrooki* (pattern 21, Fig. 31), as, for example, TNHC 4300 from Stillwater.

A specimen with data given as Bridges Pass, Wyoming (USNM 1715) is also considered an intergrade. It is a juvenile male with a pattern that appears to be intermediate between the juvenile patterns of *L.g. splendida* and *L.g. holbrooki*. The intergenials number 2 + 2. Since no additional specimens have been reported from this area or nearby, the locality data are questionable.

Lampropeltis getulus nigritus Zweifel and Norris

Lampropeltis getulus nigritus Zweifel and Norris, 1955: 238.
Lampropeltis getulus nigrita: Smith and Taylor, 1966: 23.

Holotype.—MVZ 50814 collected by Kenneth S. Norris and Richard G. Zweifel at 30.6 road miles south of Hermosillo, Sonora, Mexico.

Definition.—A subspecies of *L. getulus* characterized by a uniform black dorsum or a black ground color on which some dorsal scales and each lateral scale have a very small spot, 23 or 25 dorsal scale rows, anterior genials usually longer than posterior genials, 2 + 2 or 2 + 3 intergenials, a variable shaped loreal, and a moderately bilobed hemipenis.

Range.—Western Sonora and extreme northwestern Sinaloa, Mexico.

Description.—The following meristic and mensural data for this subspecies are based on a small sample of only 6 males and 7 females: ventrals 213 to 225 in males, 214 to 225 in females, subcaudals

52 to 56 in males, 47 to 51 in females; infralabials 9 (54.0%; or 10 (46.0%); loreal square (30.8%), slightly longer than high (30.8%), higher than long 23.0%), occasionally slightly higher than long (7.7%) or longer than high (7.7%); intergenials 2 + 2 (63.7%) or 2 + 3 (36.3%); anterior genials longer than posterior genials 42.8%), slightly longer (28.6%), or equal (28.6%); tail length 14.2% (14.1-14.4%) of total length in three males, 13.4% in one female; snout length 29.1% (28.4-29.9%) of head length in two males, 30.1% in one female.

The pattern is a reduced *L.g. splendida* pattern (pattern 25, Fig. 31), sometimes being so reduced that there is no visible pattern and the animal is uniformly black both dorsally and ventrally (pattern 26, Fig. 31). The anal plate, however, is always light colored.

Discussion.—Zweifel and Norris (1955) described *L.g. nigritus* as a subspecies which differs "from all other forms of *L. getulus* in its uniform dark brown or slaty black dorsal coloration without any trace of rings or stripes and in its high dorsal scale count." Of the 13 specimens of this subspecies examined, only two have the uniformly dark pattern 26 (Fig. 31). All others show the reduced *L.g. splendida* pattern 25 (Fig. 31). This condition is analagous to that found in *L.g. niger* with regard to the reduced *L.g. holbrooki* pattern. The high dorsal scale count reported by Zweifel and Norris (1955) resulted from their beginning their examination anterior to one head-length posterior to the head. Furthermore, occasional specimens of *L.g. splendida* also have 25 dorsal scale rows. The incidence of 25 scale rows, however, does appear to be greater in *L.g. nigritus*.

Hardy and McDiarmid (1969) reported two specimens from northern Sinaloa, Mexico, which they described as "similar to a specimen reported by Zweifel and Norris (1955: 239-40) as an intergrade between *L. getulus nigritus, L.g. splendida,* and *L.g. yumensis*." LACM 28715, one of the two specimens reported by Hardy and McDiarmid (1969) from 6 miles E Los Mochis, has a pattern only slightly bolder than pattern 25. Another specimen (LACM 52511), from 25.6 miles S Los Mochis, Sinaloa, is a large adult male (snout-vent length 1077 mm) with a typical *L.g. splendida* pattern 23. This suggests that *L.g. splendida* populations may occur south and east of this locality. Otherwise, the nearest locality for *L.g. splendida* is 6 miles E Santa Barbara in southern Chihauhua (AMNH 67731). The northern Sinaloa specimens probably represent intergrades between *L.g. splendida* and *L.g. nigritus*. All specimens north of Sinaloa to the northern third of Sonora are typical *L.g. nigritus*. Even juveniles such as USNM 148562 from 6 miles S Navajoa, Sonora, have the characteristic black pattern.

The northern one-third of Sonora and southeastern Arizona (Pima, Santa Cruz, Cochise, and southern Graham counties) is considered an intergrade zone in which specimens intermediate between *L.g. splendida* and *L.g. nigritus* are found (pattern types intermediate between 23 and 25). Within this area, specimens may have either a pattern typical of *L.g. splendida* (23) as UAZ 25127 from Cananea, Sonora, or *L.g. nigritus* (25) as AMNH 100628 from Fronteras, Sonora, or intermediate as EAL 141 from 4 miles N Nogales, Santa Cruz County, Arizona. Ecological preferences may allow the two subspecies to interdigitate in Sonora; *L.g. splendida* may occur along irrigation canals whereas *L.g. nigritus* may be confined to the desert.

Intergrades between *L.g. splendida* and *L.g. nigritus* have been found in scattered localities in southeastern Arizona as far north as Pima County (UAZ 22052 from Riletto Wash, Mt. Lemmon Road) and Cochise County (UAZ 25064 from 10 miles W Douglas). Influence of *L.g. nigritus* in Graham County has also been found and is discussed under the relationships of the *splendida* complex with the *californiae* complex.

The shape of the loreal scale cannot be used as a criterion for distinguishing either intergradation or relationships. Zweifel and Norris (1955) commented that the shape of the loreal, being somewhat longer than high in the two specimens of *L.g. nigritus* examined, "suggests relationship to *yumensis*, while the ventral counts are suggestive of *splendida*." They added that "the presence of brown centers in dark brown lateral body scales is possibly indicative of a relationship to the speckled condition of *splendida*." The loreal shape is too variable to be a reliable character. In addition, 22% of the specimens of *L.g. splendida* examined have a loreal which is longer than high.

There are still too few specimens of *L.g. nigritus* available. None the less, unless additional collecting in southern Sonora reveals specimens with the *L.g. splendida* pattern, the differentiation of this population is sufficient to warrant its recognition as a valid subspecies of *L. getulus*.

The *californiae* Complex
Lampropeltis getulus californiae (Blainville)

Coluber californiae Blainville, 1835: 292.
Ophibolus boylii Baird and Girard, 1853: 82.
Coronella balteata Hallowell, 1853: 236.
Lampropeltis boylii conjuncta Cope, 1861: 301, 305.
Coronella pseudogetulus Jan, 1863: 238, 247.
Coronella getulus californica: Jan, 1865: Part 14, Pl. 5, Fig. 3.
Ophibolus getulus conjunctus: Cope, 1875: 37, 92.
Ophibolus getulus eiseni Yarrow, 1882: 439.
Lampropeltis nitida Van Denburgh, 1895: 143.
Lampropeltis boylei: Atsatt, 1913: 41.
Lampropeltis getulus yumensis Blanchard, 1919: 70.
Lampropeltis californiae nitida: Blanchard, 1920: 3.
Lampropeltis getulus conjuncta: Blanchard, 1920: 4.
Lampropeltis getulus californiae: Klauber, 1936: 18.

Holotype.—None designated. Type locality given as "California" restricted to the vicinity of Fresno by Schmidt (1953).

Definition.—A subspecies of *L. getulus* characterized by 21 to 44 light crossbands or a vertebral stripe on a ground color of chocolate brown to black, 23 or 25 dorsal scale rows, anterior genials usually longer than the posterior genials, 2 + 3 intergenials, a longer than high loreal, and a moderately bilobed hemipenis.

Range.—Southwestern Oregon southward to extreme southern Baja California, and eastward to southern Utah and the western half of Arizona.

Description.—Ventrals 213 to 250 in males, 213 to 255 in females; subcaudals 46 to 63 in males, 44 to 57 in females; infralabials 9 (66.8%) or 10 (30.8%), rarely 8 (1.2%) or 11 (3.1%); loreal usually longer than high (44.5%), slightly longer than high (15.5%), or square (33.1%), rarely higher than long (4.3%); intergenials usually 2 + 3 (55.0%), sometimes 2 + 2 (38.0%), rarely 2 (2.8%), 1 + 2 (1.8%), 2 + 4 (1.5%), 3 (0.5%), 3 + 4 (0.2%), or 1 + 3 (0.2%); anterior genials usually longer than posterior genials (52.3%), sometimes slightly longer (26.3%) or equal (21.2%), rarely less (0.2%); tail length 13.1% (11.4-15.1%) of total length in males, 12.2% (10.5-14.3%) in females; snout length 31.1% (27.9-33.7%) of head length in males, 30.7% (28.3-33.8%) in females.

The pattern is variable and consists of two types—longitudinal stripes or dorsal crossbands. Specimens with the striped pattern occur sympatrically with the banded pattern form.

In Oregon, California, Nevada, Utah, most of Arizona, and Baja California del Norte, specimens possess the banded pattern 27 (Fig. 33) in which the scales of the bands are entirely white or yellow (Fig. 32). In occasional specimens, the dorsal bands do not extend onto the venter but stop on the first scale row (pattern 28, Fig. 33) leaving the venter uniformly black. The bands may be connected along the first scale row to form lateral stripes. Specimens from southwestern Arizona, southern California, and Baja California (especially Baja California del Sur) usually have a pattern in which the scales of the dorsal bands are dark edged (pattern 29, Fig. 33). In southern Arizona, these bands may be narrow (pattern 30, Fig. 33).

The striped pattern 32 (Fig. 33) is found on specimens from southern

California and Baja California del Norte. The venter is usually light, but the dark edges of each ventral scute may extend farther toward the midline. Pattern 31 (Fig. 33) differs from the preceding primarily by the absence of lateral spotting (replaced by lateral stripes) and possession of a uniformly dark venter. Specimens with this pattern are found only in southern Baja California del Sur.

Discussion.—Although distinctive pattern types are found among populations of *L.g. californiae*, the division of these populations into subspecies cannot be justified. Pattern variation is either clinal or more than one type occurs within a single population.

Blanchard (1919) described *L.g. yumensis* as differing from the typical banded form (*L.g. boylii*) in that the scales of the bands "are shaded basally with brown, thus giving a spotted appearance to the light annuli," patterns 29 and 30 (Fig. 33). Klauber's (1936) concept of *L.g. yumensis* was somewhat more restrictive than Blanchard's (1919) description. Klauber characterized this subspecies, based primarily on specimens from the vicinity of Yuma, as having a pattern in which "the light rings are narrow and only the centers of the scales in these rings bear the light color." Specimens of this pattern (30) represent the greatest reduction of the basic banded pattern (27) and, especially in the vicinity of Yuma, may be the result of influence from *L.g. nigritus*, as is discussed under the relationship of the *californiae* complex to the *splendida* complex, below. Between Tucson and Yuma, many specimens possess a pattern of broader bands but with the same spotted appearance (pattern 29, Fig. 33). The distribution of these pattern types, of the continuous banded pattern (27), and of patterns intermediate between types 27 and 29, is shown in Fig. 34. It is obvious that the distributions of the two patterns broadly coincide, and that *L.g. yumensis* should not be recognized.

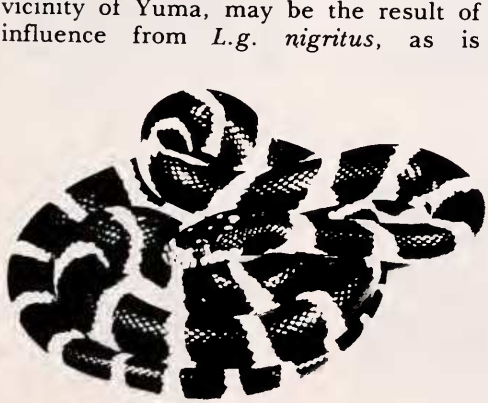


Figure 32. *Lampropeltis getulus californiae* from Cottonwood, Yavapai County, Arizona (specimen not available).

The population of banded kingsnakes in the Cape region of Baja California del Sur has been recognized as a distinct subspecies, *L.g. conjuncta* (Cope). The dorsal pattern is identical to that of *L.g. yumensis* (pattern 29), but the two forms were said to differ in that the "white bars on the prefrontal plates are oblong and occupy not more than one-half the area of these scutes" in *L.g. yumensis*, and "furthermore, in *L. getulus conjuncta* the infralabials are usually 10, and in *L. getulus yumensis* they are usually 9" (Blanchard, 1919). I have found that the width of the prefrontal bars decreases clinally from northwest to southeast. Even in central California, however, specimens with pattern 29 also have a more reduced prefrontal bar than specimens with pattern 27 from the same locality. This follows because the dorsal pattern reduction is due to increased melanin, and other pattern features, including the prefrontal bar, are likewise reduced. The banded populations in southern Baja California also have a reduced prefrontal bar (occupying 50 to 70% of the prefrontal scale compared with 80 to 95% in banded specimens with pattern 27), but the reduction is not so great as in southern Arizona. The latter may be the result of the influence of *L.g. nigritus*. The difference in the number of infralabials must be discounted. As was discussed above (variation in infralabials), all the populations in Baja California, including specimens with continuous bands in Baja California del Norte, have an unusually high incidence of 10 infralabials (more than 50% of the specimens examined). Hence, the southern Baja California population does not differ significantly from populations in southern Arizona and California, and therefore should not be recognized as distinct.

Occasional specimens of *L.g. californiae* are found with pattern 28 (Fig. 34). Some specimens with this pattern type have the lateral edges of the bands expanded to form a pair of lateral stripes (*i.e.*, MVZ 64873 from 1 mile W Michigan Bar, Sacramento County, California) and were considered to belong to the striped species, *Lampropeltis californiae*, by Blanchard (1921) and Van Denburgh (1922). This pattern formed the basis of the description of *Ophibolus getulus eiseni* Yarrow, 1882. It is apparent that this form of striping is not homologous with the striping found in specimens in southern California (pattern 32), but rather is aberrant and derived from the typical banded pattern 27. Localities for specimens exhibiting this pattern are shown in Fig. 35.

The striped patterns 31 and 32 are found in southern Baja California and southern California, respectively (Fig. 35). Patterns intermediate between these patterns and the sympatric banded patterns are found in the same localities. Klauber (1936, 1939, 1944) provided considerable evidence that the striped form (*Lampropeltis californiae*) and the banded form (*Lampropeltis getulus boylii*) are pattern phases of a single subspecies, *L.g. californiae*. His conclusions were based primarily on a large series of broods from San Diego County, California, in which both pattern types appeared regardless of the pattern types of the mother. By analogy, Klauber (1936) suggested that *L. nitida* of southern Baja California was a pattern phase of *L.g. conjuncta*. However, since he also questioned the validity of *L.g. conjuncta*, he suggested "that all of these king snakes should be referred to as *L.g. californiae*." A specimen of *L. getulus* (LACM 21450) from Los Martiles, 5 miles S Buena Vista (Rancho), Baja California del Sur, Mexico, has a mixed pattern of

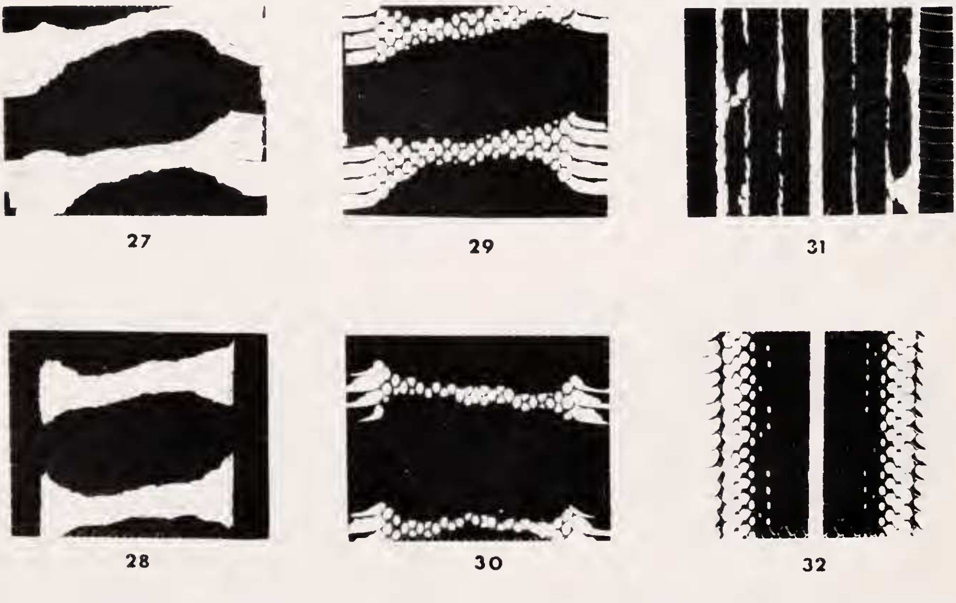


Figure 33. Basic pattern types of the *californiae* complex of *Lampropeltis getulus*. Striped and banded patterns of *L.g. californiae*.

crossbands and stripes, much like the mixed pattern found on some specimens in southern California, except that the venter is dark. Anteriorly, three bands (pattern 29) are complete; posteriorly, the dorsal stripe is broken in several places, but the pattern is essentially like pattern 31. The presence of this mixed pattern supports Klauber's contention that *L. nitida* is a pattern phase of the southern Baja California banded form. Thus, all of these populations are considered to be *L.g. californiae*.

Soule and Sloan (1966) reported *L.g. californiae* from several islands in the Gulf of California. Two specimens (SDSNH 44631 and 44632) from the northern end of Monserrate Island, Baja California del Sur, are typical of the southern Baja California population (pattern 29). The number of ventrals, however, is higher (223 on SDSNH 44631, a male, and 240 on SDSNH 44632, a female) and there are more dorsal bands (39 on each). In addition, shed skins were found on three islands in the northern Gulf of California: SDSNH 19989 from Isla Angel de la Guarda; SDSNH 45003 from Salsipuedes Island; SDSNH 45150 from Isla San Lorenzo Norte. SDSNH 19989 and 45003 clearly are *L.g. californiae* and pattern 29 can be detected in the shed skins. However, SDSNH 45150 does not have a distinctive pattern of crossbands. The skin appears to have come from a snake with a light venter (except for the lateral margins of the ventral scutes which are dark), light lateral scales, and a dark vertebral stripe. Other characteristics indicate that the skin came from a *Lampropeltis*, but its identification remains questionable.

Another kingsnake was reported from Cerralvo Island, east of La Paz, as *Lampropeltis getulus conjuncta* (Figg-Hoblyn and Banta, 1957). This specimen (not examined) appears to agree with the population on the adjacent mainland.

Klauber (1939) submitted the proposition that the populations of kingsnakes on southern California and northern Baja California which had the potential to "produce striped and aberrant pattern phases" might be recognized as a distinct

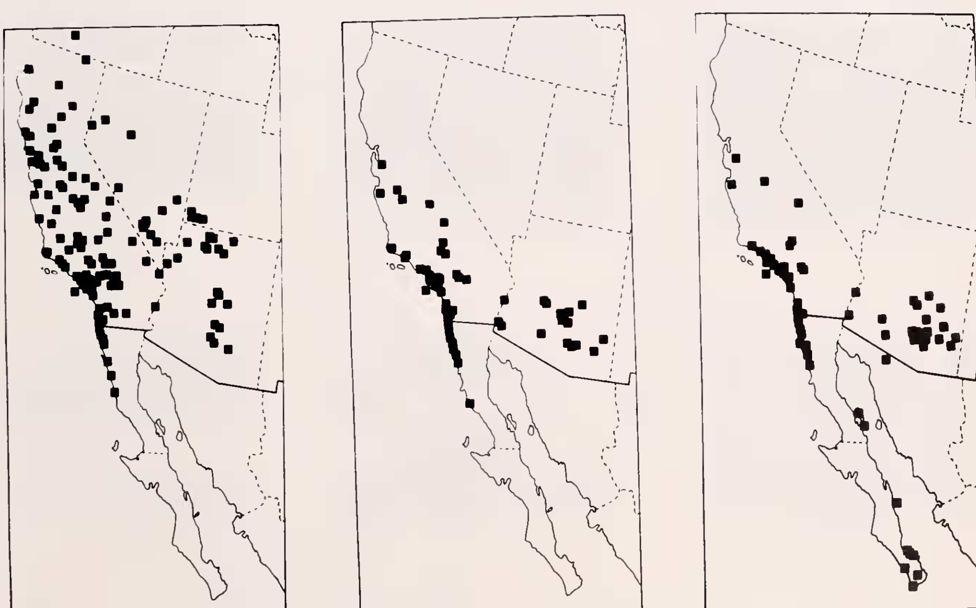


Figure 34. Distribution of the banded pattern types of *Lampropeltis getulus californiae* (left, pattern 27; right, pattern 29; middle, patterns intermediate between patterns 27 and 29).

subspecies. He presented one objection, however, with which I completely agree, that the classification of banded individuals would be based entirely on locality. Hence, I consider all of these populations to be *L.g. californiae*, a highly variable subspecies in which slight differentiation of the pattern has resulted in some recognizable populations. However, the degree of differentiation, relative to other subspecies within *L. getulus*, is at most at the level of the microgeographic race. The significance of the striped and banded pattern types is discussed in the conclusion section.

Relationships with the *splendida* Complex

Intergradation between *L.g. californiae* and members of the *splendida* complex occurs in southeastern Arizona and the southern Colorado River basin. Thirty-eight intergrades have been examined from this narrow zone.

L.g. californiae and *L.g. nigritus* intergrade along the Colorado River Valley and in southeastern Arizona. Such intergrades exhibit a darkened *L.g. californiae* pattern (pattern 33, Fig. 36) and have been found as far north as Parker, Yuma County, Arizona (ASU 4313). Three other specimens in the Colorado River Valley (UMMZ 69656 from the Gila Valley, near Yuma, Yuma County, Arizona; MVZ 32009 from the Laguna Dam, Potholes, Imperial County, California; and LACM 21449 from immediately west of the Rió Colorado on Mexico Route 2, Baja California del Norte, Mexico) are unquestionably intergrades (pattern 33). However, eight additional specimens from the Colorado River Valley are typical *L.g. californiae* (pattern 29): KU 90837, UAZ 25084-25085, and MCZ 27107, all from Yuma, Yuma County, Arizona; UIMNH 38729 from 1.5 miles E Laguna, Yuma County, Arizona; MVZ 49932 from 7.3 miles SSW Imperial Dam, Imperial County, California; LACM 21437 from 5 miles S Alligator Slough (north of Blythe); and MVZ 5543 from 14 miles NE Blythe, Riverside County, California.

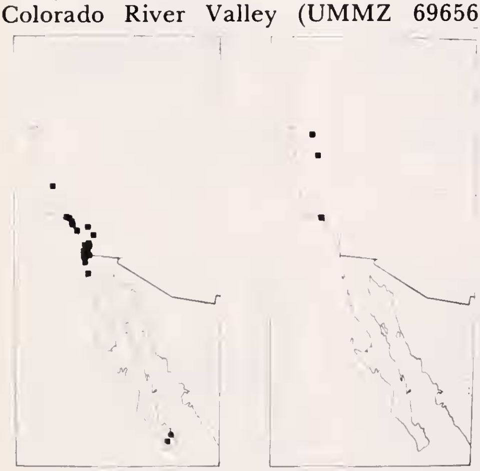


Figure 35. Distribution of the striped and black-bellied banded patterns of *Lampropeltis getulus californiae*. Left, the striped patterns 31 (circles) and 32 (squares); right, pattern 28.

The narrow bands (pattern 30) found on some specimens of *L.g. californiae* may reflect the influence of *L.g. nigritus* populations to the south. However, some specimens with the continuous banded pattern 27 also have narrow bands (*i.e.*, ASU 308 from Phoenix, Maricopa County, Arizona), and pattern 30 is also found as far north as Phoenix (*i.e.*, SM 1708).

Three specimens from Pima County, Arizona (ASDM 1919 from near Sasabee, UAZ 25075 from 0.6 miles W Robles P.O., and UAZ 28605 from Tucson) have a darkened *L.g. californiae* pattern typical of intergrades with *L.g. nigritus* (pattern 33).

Intergrades between *L.g. californiae* (pattern 29) and *L.g. splendida* (pattern 23) typically have broad dorsal crossbands which fork laterally, and spotting between the bands on the lateral scale rows (pattern 34, Fig. 36). Specimens with such a pattern have been examined from Pima, Cochise, and Graham counties, Arizona. Among 61 specimens examined from the vicinity of Tucson, Pima County, 41% have pattern 29, 36% have pattern 34 (intergrades), 6.5% have pattern 33 (intergrades), 11.5% have pattern 23 or a pattern intermediate between 23 and 25, and an additional 5% have a darkened pattern 34 (three way intergrades between *L.g. californiae*, *L.g.*

nigritus, and *L.g. splendida*: LACM 52518 from 2.5 miles S Sahuarita, UAZ 25641 and 28574 from Tucson).

In Cochise County, only 8 of the specimens are intergrades between *L.g. californiae* and *L.g. splendida*, whereas 70% are either *L.g. splendida* (10 specimens), *L.g. splendida* X *L.g. nigritus* (8 specimens), or *L.g. nigritus* (1 specimen). The following specimens from Cochise County are cited:

L.g. californiae X *L.g. splendida*—SE Willcox near the Chiricahua Mountains (LACM 58902); 11.5 miles SW Willcox (UAZ 25074); 4 miles NE Chiricahua (UMMZ 83967); 2.5 miles E Pearce (UMMZ 102435); 5 miles NNW Pearce (KU 68922); 4 miles SSE Cochise (AS 118); 4 miles SW Portal (UMMZ 83967); 24 miles E Dos Cabezas (LACM 20353).

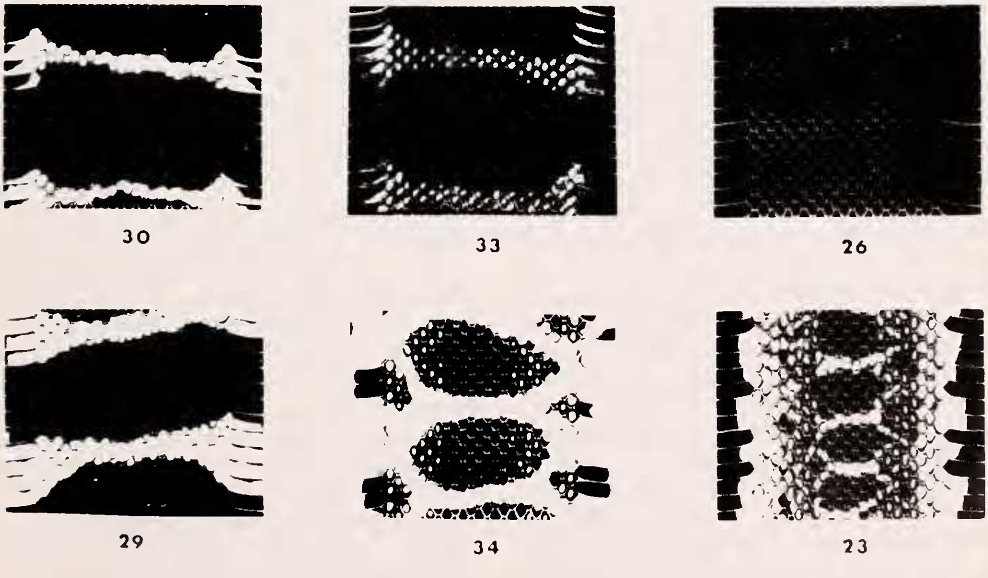
L.g. splendida—1 mile S McNeal, Rt. 666 (ASDM 1256-1258); 2.5 miles S Rodeo (UAZ 31293); 15 miles S Rodeo (KU 6652); 1.6 miles W Pearce (UAZ 25057); Apache (UAZ 25051); Bisbee (UNM 12148); 16.6 miles N Douglas (LACM 34919); 10 miles SE Willcox (UMMZ 71343).

L.g. splendida X *L.g. nigritus*—Hereford (KU 48929); 15 miles S Rodeo (KU 6651); 8 miles SW, 9.7 miles SSE Willcox (LSUMZ 23271); 0.6 miles N Bernadino (LSUMZ 8928); 1 mile NW St. David (LSUMZ 9994); 10 miles W Douglas (UAZ 25064); 1.3 miles NE Chiricahua (UAZ uncatalogued); 3.5 miles W Rt. 666, S McNeal (ASDM 1596).

L.g. nigritus—Hereford (KU 48927).

From Graham County, one specimen of *L.g. californiae* (UAZ 25050 from 6 miles S Safford), one specimen of *L.g. splendida* (UAZ 25096 from 5 miles S Safford), one intergrade between *L.g. californiae* and *L.g. splendida* (UIMNH 24558 from 5 miles S Safford), and one intergrade between *L.g. californiae* and *L.g. nigritus* (AMNH 95953 from 5 miles N Solomon on the north bank of the Gila River) have been examined.

Thus, southeastern Arizona is an area of intergradation between *L.g. californiae*, *L.g. splendida*, and *L.g. nigritus*. The scattered records in a relatively narrow area, however, reflect the divergence of the two groups.



30 33 26

29 34 23

Figure 36. Pattern types of intergrades between *Lampropeltis getulus californiae* and members of the *splendida* complex. Pattern 29, *L.g. californiae*; pattern 33, intergrade between *L.g. californiae* and *L.g. nigritus*; pattern 34, intergrade between *L.g. californiae* and *L.g. splendida*; pattern 26, *L.g. nigritus*; pattern 23, *L.g. splendida*.

SUMMARY AND CONCLUSIONS

Color pattern is the primary feature on which I base my hypotheses about ancestral *Lampropeltis getulus* populations. Theoretically, the primitive pattern must be one from which all other patterns could have been derived. I suggest that pattern 24, as exhibited by *L.g. splendida* is closest to the ancestral type. In addition, I regard the high number of dorsal scale rows in *L.g. splendida* as a primitive character and its hemipenial structure as both primitive and generalized. Consequently, I consider *L.g. splendida* to be closest to the ancestral line. Moreover, the geographic position that *L.g. splendida* now occupies is one from which most other populations could have dispersed and differentiated.

A very early radiation of *L. getulus* produced three distinct phylogenetic lines, the *getulus* complex in the east, the *californiae* complex in the west, and the centrally located *splendida* complex. A proposed phylogeny for *Lampropeltis getulus* is illustrated in Fig. 37.

The primitive pattern (24) of *L.g. splendida* has been modified slightly by the reduction of spotting between the dorsal bands to produce pattern 23. At the present time, only occasional specimens exhibit pattern 24. The differentiation of the other subspecies in the *splendida* complex has followed obvious lines. The evolution of *L.g. nigritus* in the Sonora Desert reflects a darkening of the *L.g. splendida* pattern but with no change in scutellation. The differentiation of *L.g. holbrooki* has involved slight modification of the primitive pattern, and a reduction in the number of dorsal scale rows and intergenials. The evolutionary processes of pattern neoteny and melanization produced *L.g. niger*.

The wide zone of intergradation between *L.g. holbrooki* and *L.g. splendida* in Oklahoma and Kansas may be the result of population displacement during the Late Wisconsin glaciation and the subsequent repopulation of an area of interdigitated deciduous forest and grassland habitats (Küchler, 1964). During the retreat of the glaciers, populations of both subspecies may have moved into this region. The result is a heterogenous series of populations with widespread intergradation.

The greatest distributional anomaly in the *splendida* complex is the presence of *L.g. splendida* on Santa Catalina Island in the Gulf of California, Mexico. Whether this record represents a relict population or a rafted or released individual remains to be proved. The possibility of there being a relict population on Santa Catalina Island seems remote since *L.g. californiae* occurs on Monserrate Island, just 15 miles west of Santa Catalina Island. This record must remain questionable until additional specimens become available.

Blanchard (1921) postulated that *L.g. getulus* was derived from *L.g. niger* by expansion of the light dorsal bands and that *L.g. floridana* evolved from *L.g. getulus* by "a basal lightening of each dark scale." His evidence for such a phylogeny, however, was based primarily on the geographic position of these forms. First, he considered that *L.g. getulus* was derived from *L.g. niger* because of similarity of pattern and because the two populations are adjacent. I have shown that his interpretation of pattern similarity is unwarranted; the reduced number of dorsal bands in *L.g. niger* is not an approach to the condition in *L.g. getulus*. Furthermore, the great difference in hemipenial structure between *L.g. getulus* and *L.g. niger* also eliminates *L.g. niger* as a probable ancestor. In addition, the lack of a wide zone of intergradation between the two forms indicates that *L.g. getulus* and *L.g. niger* are not closely related.

Within the *getulus* complex, I consider *L.g. floridana* to be closest to the ancestral stock, a direct derivative of the primitive *L.g. splendida* populations in Texas. I base this hypothesis on both populations having a maximum of 23 dorsal scale rows, and similarities in dorsal pattern. The *L.g. floridana* pattern is interpreted as being the result of an ontogenetic increase in scale spotting on

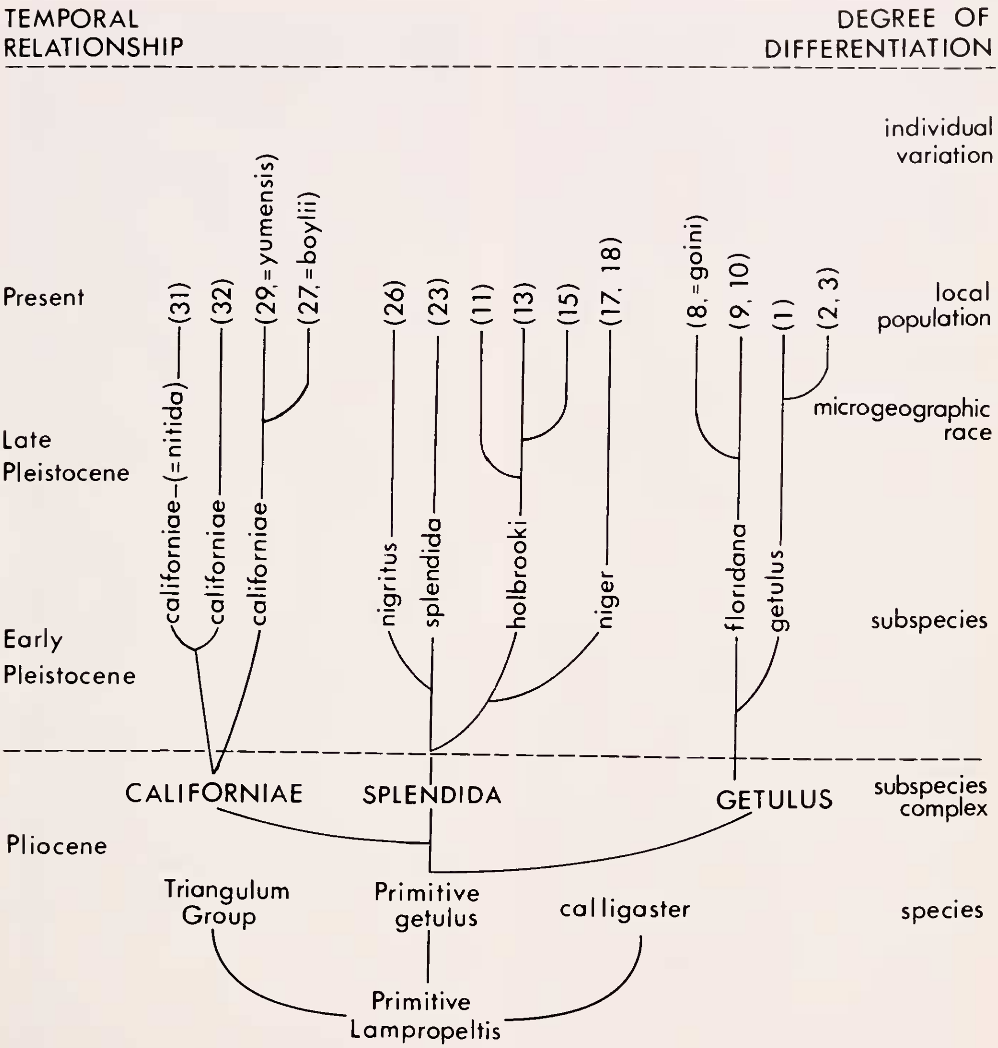


Figure 37. A proposed phylogeny for the subspecies and microgeographic races of *Lampropeltis getulus*. Numbers in parentheses at top refer to pattern types.

the basic primitive pattern. The pattern of *L.g. getulus* is the result of retention of the juvenile pattern of *L.g. floridana*. Additionally, *L.g. getulus* has fewer dorsal scale rows (21 compared with 23).

The geographic separation between *L.g. floridana* and *L.g. splendida* does not exclude the possibility of the proposed phylogenetic relationship. I suggest that the population ancestral to *L.g. floridana* (similar in pattern to *L.g. splendida*) expanded its range from the west into the land newly exposed by a reduction of Pleistocene sea level (Russell, 1964). Such a migration probably occurred during a glacial stage prior to the Wisconsin glaciation. It has been suggested that *Terrapene carolina* (Auffenberg, 1958; Blaney, 1971), *Coluber constrictor*, and *Masticophis flagellum* (Blaney, 1971) have also utilized such a Pleistocene migration route. The presence of disjunct populations of *L.g. floridana* in northeastern Florida and in the Apalachicola region suggest that *L.g. floridana* was once widespread throughout the peninsula. Rising seas of an interglacial stage then isolated the eastern (*L.g. floridana*) and western (*L.g. splendida*) groups by inundation of the continental shelf. Perhaps at the same time, spatial separation of the northern and southern extremes of the eastern group resulted in differentiation into the two subspecies now recognized (*L.g. getulus* and *L.g. floridana*). Partial inundation of the Okeefenokee region may have resulted in at least some degree of isolation of the two populations. During the successive glacial stage, the *L.g. floridana* population in the northern Florida peninsula moved south following suitable habitat. At the same time, the newly differentiated *L.g. getulus* moved into the northern part of the peninsula, intergrading with and replacing *L.g. floridana*, thus producing the wide zone of intergradation now observed. The *L.g. getulus* stock probably moved along the central highland region of Florida thus separating the northern populations of *L.g. floridana*—the Apalachicola population and the northeastern Florida population. The disjunct *L.g. floridana* population in the Apalachicola region has undergone some differentiation which is reflected in the wide dorsal bands, but, as discussed above, the population consists of intergrades and should not be given taxonomic recognition.

Additional evidence that it was *L.g. getulus* which differentiated from *L.g. floridana* is provided in the occasional individuals and populations (*i.e.*, the Outer Banks of North Carolina) which show characteristics of *L.g. floridana*. The populations of *L.g. getulus* have undergone a further differentiation into two microgeographic races, a piedmont and a coastal form. The populations in Maryland and Delaware are derived from the piedmont form. The New Jersey populations, on the other hand, are coastal plain derivatives.

The reduced amount of intergradation occurring between *L.g. getulus* and members of the *splendida* complex may be the result of the population displacements discussed above. *L.g. getulus, L.g. holbrooki*, and *L.g. niger* probably have expanded their ranges since the last glaciation. The populations of *L.g. holbrooki* and *L.g. niger* may be only now making contact with *L.g. getulus*.

The evolution of *L.g. californiae* has involved various modifications of the primitive *L.g. splendida* pattern. Blanchard (1921) used characteristics of intergradation as evidence for the evolution of *L.g. yumensis* (=*L.g. californiae*) from *L.g. splendida*. The banded pattern of *L.g. californiae* probably was derived in a fashion very similar to that which he described. The dorsal bands of *L.g. splendida* increased in length as the lateral spotting between the bands decreased, until the dorsal bands extended onto the ventral scutes. Within the *californiae* complex, therefore, I consider pattern 29 to be closest to the primitive banded pattern. The continuous banded pattern 27 is a further specialization of this basic pattern.

Concerning the striped pattern exhibited by *L.g. californiae*, Blanchard (1921) stated that this form (which he considered as a species) was derived from animals with the continuous banded pattern. He based this contention on the aberrant striped individuals that approach the continuous banded pattern. Blanchard presented the hypothesis that the striped pattern types resulted from a mutation of the continuous banded form, because the striped pattern apparently became differentiated within the range of its parent. Thus he said that the striped form originated "somewhere in the Great Valley of California. It spread southward west of the Sierra Nevada Mountains and the deserts of southwestern California, becoming more different from *boylii* toward southwestern California. From here it extended its range into Lower California to Cape San Lucas. At some point in this peninsula, probably pretty well south, it became modified into the color variety *nitida*." If one accepts the well documented idea that the striped and banded patterns occur in a single species (Klauber, 1936, 1939, 1944), the above concept does not explain the fact that in San Diego County 90% of the kingsnakes exhibit either the banded or the striped pattern and only 10% have a mixed pattern, whereas populations to the north in Orange, Riverside, and Los Angeles counties are different in the relative abundance of these patterns. In the San Diego area, the striped pattern comprises about one third of the population, and the striped pattern outnumbers the mixed pattern by 3 or 4 to 1 (Klauber, 1936). In Orange, Riverside and Los Angeles counties, however, only 6% of the population show any tendency toward striping and the mixed pattern is five times more abundant than the striped pattern. The evolution of these striped populations that are sympatric with banded populations has also not been adequately explained.

Dunn (in Mayr, 1944) attempted to prove that the segregation of striped and banded pattern types indicated a simple Mendelian relationship involving a single pair of genes. The ratios within broods of banded mothers indicated that the banded pattern is dominant, but the progeny of striped mothers did not approach expected frequencies. Klauber (1936) showed that the young from banded mothers were mostly banded, whereas the young of a striped mother are mostly striped. Dunn (*loc. cit.*) included the aberrant patterns among the striped "because of the resemblance of the aberrant to the general features of the striped form" and stated that there was "no indication that the aberrants are hybrids." He neglected to note the fact that in populations immediately north of San Diego, the aberrant patterns are far more abundant. In these areas and in San Diego County, the so-called aberrant patterns range from banded with occasional bands broken (some of which may be oriented longitudinally) to essentially striped with the vertebral stripe broken (some of the smaller sections of the stripes may be oriented laterally). I do not recognize these patterns as aberrant, but rather as intermediate between the striped and banded patterns. The range of variation among specimens exhibiting the intermediate pattern indicates that more than a single pair of genes is responsible for the two pattern types, and therefore this phenomenon is not a simple pattern dimorphism. The full range of intermediate patterns between the two extremes indicates that there are at least two, and probably more, alleles responsible for pattern. Pattern modifying genes may cause varying degrees of expression of other genes. It appears, then, that there is no simple Mendelian relationship between the two pattern types.

The fact that few intermediates exist in San Diego County perhaps can be attributed to environmental factors that prevent the action of some pattern modifying genes. Thus, the pattern expression is an either-or situation with only occasional action of modifying genes resulting in only 10% of the population being intermediate. The populations in San Diego County therefore approach true pattern dimorphism. Elsewhere, because of the high incidence of intermediates, the situation is certainly not a simple dimorphism, nor can it be called polymorphism because the additional patterns are not something new, but rather something intermediate. Such a range of variation in pattern might be expected in a zone of intergradation between two subspecies.

I suggest, therefore, that the existence of these two very different pattern types may be the result of two different phylogenetic lines, and the intermediate specimens are actually the result of intergradation. Population movements and displacement may have resulted in these two lines competing for and occupying the same geographic area. Thus we may actually be observing what were once two subspecies occurring sympatrically at the present stage in their evolution.

Two lines may have diverged from the primitive *L.g. splendida* stock, the banded pattern type in the manner previously described and the striped pattern by a rather simple modification of the *L.g. splendida* pattern. The dorsal bands of *L.g. splendida* need only to have become oriented longitudinally and the lateral spotting reduced slightly. The ventral coloration probably was dark primitively (retained in the populations in southern Baja California and occasional specimens in southern California), but became light as the pattern became more specialized. The striped populations probably became established in southern California and extended into Baja California. This striped population then became separated into southern California and southern Baja California populations, each of which differentiated, thus producing the two distinctive striped populations. Meanwhile, the banded populations differentiated farther east and north. Fluctuations in climate and sea level during the Pleistocene may have caused displacement of the banded populations.

The banded populations in southeastern California and southwestern Arizona may have expanded southward along the eastern coastal shelf (exposed during a glacial period in the Late Pleistocene) of the Baja California peninsula thus invading the southern part of the peninsula which was already occupied by a striped population. Evidence for such a hypothesis is the occurrence of *L.g. californiae* with pattern 29 on the islands in the Gulf of California. Perhaps at the same time, the central California banded populations expanded their range southward and invaded the territory already occupied by striped populations in southern California. In each case, the result is intergradation not at the periphery of the range of these forms, but within the range of the striped form. At present, then, we may be looking at the replacement of a striped population by a banded population.

Nomenclatural recognition of such a situation is impossible. Although it is possible to distinguish two populations of striped kingsnakes, both are found sympatrically with banded forms. In southern Baja California, the striped form (*L.g. nitida—L.g. californiae*) is found within the banded population (*L.g. conjuncta = L.g. yumensis = L.g. boylii = L.g. californiae*) similar to the population in southwestern Arizona. The southern California striped populations (*L.g. californiae*) are sympatric with banded forms having pattern types 27 and 29 (*L.g. boylii* and *L.g. yumensis = L.g. californiae*). Thus, to avoid recognition of sympatric subspecies, all populations must be regarded as part of a diphyletic subspecies, *L.g. californiae*.

Neill (1963) provided a substantial amount of information on the occurrence of striped patterns in the eastern subspecies of *L. getulus*, stating that the "lineate, '*californiae*' pattern is often suggested, and sometimes duplicated." Thus Neill (1963) postulated "that a single widespread species, *L. getulus*, has the genetic potentiality of producing a lineate pattern along with the more common ringed one." Many individuals of *L.g. getulus* have incomplete dorsal bands, perhaps half a band reaching only the middorsal scale row. The bands of others may be broken and longitudinally expanded. The lateral forking of the dorsal bands may be so prominent so as to form a continuous lateral line. The specimen illustrated by Neill (1963: 198 A) has an almost continuous vertebral stripe, but it is not identical to the vertebral stripe exhibited by *L.g. californiae*. A specimen from near Engelhard, Hyde County, North Carolina (NCSM 2019), also has an aberrant striped pattern. This specimen has no light dorsal bands, but rather has paired lateral blotches that are connected along the fourth scale rows on each side by a continuous light stripe. Thus, this specimen has a pair of dorsolateral stripes. It would appear, then, that the pattern of dorsal bands lends itself to aberrations that may take the form of longitudinal stripes.

Analysis of distribution.—The overall range of *L. getulus* may be limited by two factors: 1) competition with similar species; and 2) a reflection or Pleistocene displacement southward. The northern extremes of the range may be the result of the displacement of the species southward during the Late Wisconsin glaciation in conjunction with thermal factors. *L.g. californiae* is not common in northern California and Oregon. The northern limits of *L.g. holbrooki* and *L.g. niger* may reflect glacial displacement followed by a slow recovery of territory. The distribution of *L.g. getulus* along the Atlantic coast may reflect the same phenomenon. There are records of *L.g. getulus* from Long Island (DeKay, 1842) and New England (Babcock, 1920). Babcock (1920) said, however, that the occurrence of *L.g. getulus* in Connecticut, based on a sight record, is doubtful. Nonetheless, it is possible that the range of *L.g. getulus* did extend this far north at one time, but that such populations are now extinct.

I suggest that the northern limits of *L.g. getulus, L.g. niger,* and *L.g. holbrooki*, and the southern limit of *L.g. splendida* in Mexico, may be affected by competition with populations of large-sized *Lampropeltis triangulum*. The large *L.t. triangulum* replaces *L. getulus* in the northeastern United States and *L.t. polyzona, L.t. arcifera, L.t. nelsoni,* and *L.t. sinaloae* replace *L.g. splendida* in Mexico (distribution based on Williams, 1970).

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LITERATURE CITED

Allen, E.R., and W.T. Neill. 1954. Juveniles of Brooks' Kingsnake, *Lampropeltis getulus brooksi*. Copeia 1954 (1): 59.

Anderson, P. 1965. The reptiles of Missouri. Univ. Missouri Press, Columbia, Missouri. xxii + 330p.

Atsatt, S.R. 1913. The reptiles of the San Jacinto area of southern California. Univ. California Publ. Zool. 12(3): 31-50.

Auffenberg, W. 1958. Fossil turtles of the genus *Terrapene* in Florida. Bull. Florida State Mus. 3(2): 53-92.

............1963. The fossil snakes of Florida. Tulane Studies Zool. 10(3): 131-216.

Babcock, H.L. 1920. Some reptile records from New England. Copeia 1920(85): 73-76.

Bailey, V. 1905. Biological survey of Texas. North Amer. Fauna(25). 222p.

Baird, S.F., and C. Girard. 1853. Catalogue of North American reptiles in the museum of the Smithsonian Institution. Part 1-Serpentes. Smithsonian Inst., Washington, D.C. xvi + 172p.

Barbour, T. 1919. Another new race of the king-snake. Proc. New England Zool. Club 7: 1-3.

............and W.L. Engels. 1942. Two interesting new snakes. Proc. New England Zool. Club 20: 101-104.

Blainville, H.D. de. 1835. Description de quelques especes de reptiles de la Californie. Nouv. Ann. Mus. d'Hist. Paris 4: 233-296.

Blanchard, F.N. 1919. Two new snakes of the genus *Lampropeltis*. Occ. Papers Mus. Zool. Univ. Michigan 70: 1-12.

............1920. A synopsis of the king snakes: genus *Lampropeltis* Fitzinger. Occ. Papers Mus. Zool. Univ. Michigan 87: 1-6.

............1921. A revision of the king snakes: genus *Lampropeltis*. Bull. U.S. Nat. Mus. 114: 1-260.

Blaney, R.M. 1971. An annotated check list and biogeographic analysis of the insular herpetofauna of the Apalachicola Region, Florida. Herpetologica 27(4): 406-430.

Blatchley, W.S. 1891. Notes on the batrachians and reptiles of Vigo County, Indiana. J.

Cincinnati Soc. Nat. Hist. 14: 22-35.
Brattstrom, B.H. 1953a. Records of Pleistocene reptiles and amphibians from Florida. Quart. J. Florida Acad. Sci. 16(4): 243-248.
...........1953b. Records of Pleistocene reptiles from California. Copeia 1953(3): 174-179.
...........1953c. The amphibians and reptiles from Rancho La Brea. Trans. San Diego Soc. Nat. Hist. 11(4): 365-392.
...........1954. Amphibians and reptiles from Gypsum Cave, Nevada. Bull. S. California Acad. Sci. 53(1): 8-12.
...........1955. Records of some Pliocene and Pleistocene reptiles and amphibians from Mexico. Bull. S. California Acad. Sci. 54: 1-4.
...........1967. A succession of Pliocene and Pleistocene snake faunas from the high plains of the United States. Copeia 1967(1): 188-202.
Brown, A.E. 1901. A review of the genera and species of American snakes north of Mexico. Proc. Acad. Nat. Sci. Philadelphia 53: 10-11.
Carr, A. 1940. A contribution to the herpetology of Florida. Univ. Florida Publ., Biol. Ser. 3(1): 1-118.
...........and C.J. Goin. 1959. Guide to the reptiles, amphibians and freshwater fishes of Florida. Univ. Florida Press, Gainesville. ix + 341p.
Clark, R.F. 1949. Snakes of the hill parishes of Louisiana. J. Tennessee Acad. Sci. 24(4): 244-261.
Cliff, F.S. 1954. Snakes of the islands in the Gulf of California, Mexico. Trans. San Diego Soc. Nat. Hist. 12(5): 67-98.
Conant, R. 1958. A field guide to reptiles and amphibians of the United States and Canada east of the 100th meridian. Houghton Mifflin Co., Boston xv + 366p.
Cope, E.D. 1861. Contributions to the ophiology of Lower California, Mexico and Central America. Proc. Acad. Nat. Sci. Philadelphia. 13: 292-306.
...........1875. Check list of North American Batrachia and Reptilia. Bull. U.S. Nat. Mus. 1: 1-104.
...........1880. On the zoological position of Texas. Bull. U.S. Nat. Mus. 17: 1-51.
Cunningham, J.D. 1959. Yosemite's king snakes. Yosemite Nat. Notes 38: 26.
DeKay, J.E. 1842. Zoology of New York. Reptiles and amphibians, *In* Natural History of New York, pt. 3. 415p.
Dessauer, H.C., and W. Fox. 1958. Geographical variation in plasma protein patterns of snakes. Proc. Soc. Exp. Biol. Med. 98: 101-105.
Dowling, H.G. 1951a. A proposed method of expressing scale reductions in snakes. Copeia 1951(2): 131-134.
...........1951b. A proposed standard system of counting ventrals in snakes. Brit. J. Herpetol. 1: 97-99.
Duellman, W.E., and A. Schwartz. 1958. Amphibians and reptiles of southern Florida. Bull. Florida State Mus. 3: 181-324.
Duges, A. 1897. Description d'um Ophidien nouveaux du Mexique (*Oreophis boulengeri*, g. et. sp. nn.). Proc. Zool. Soc. London. 1897: 284-285.
Eaton, T.H., Jr. 1970. Evolution. Norton, New York. xi + 270p.
Figg-Hoblyn, J.P., and B.H. Banta. 1957. *Lampropeltis getulus conjuncta* (Cope) on Cerralvo Island, Gulf of California, Mexico. Herpetologica 13(3): 192.
Fitzinger, L.J.F.J. 1843. Systema Reptilium. Vienna.
Hallowell,E. 1853. On some new reptiles from California. Proc. Acad. Nat. Sci. Philadelphia 6: 236-238.
Hamilton, W.J., Jr. and J.A. Pollack. 1956. The food of some colubrid snakes from Fort Benning, Georgia. Ecology 37: 519-526.
Hardy, L.M., and R.W. McDiarmid. 1969. The amphibians and reptiles of Sinaloa, Mexico. Univ. Kansas Publ. Mus. Nat. Hist. 18(3): 39-252.
Harlan, R. 1827. Genera of North American reptiles, and a synopsis of the species. J. Acad. Nat. Sci. Philadelphia 6: 317-372.
Holbrook, J.E. 1842. North American Herpetology. Philadelphia, 2nd ed. Vol. 3. 128p.
Holman, J.A. 1958. The Pleistocene herpetofauna of Saber-tooth Cave, Citrus County, Florida. Copeia 1958(4): 276-280.
...........1964a. Pleistocene amphibians and reptiles from Texas. Herpetologica 20(1): 73-83.
...........1964b. Fossil snakes from the Valentine Formation of Nebraska. Copeia 1964(4): 631-637.
Hurter, J., and J.K. Strecker. 1909. The amphibians and reptiles of Arkansas. Trans. Acad. Sci. St. Louis 18(2): 11-27.
Jan, G. 1860-1866. Iconographie générale des ophidiens. Milan. Vol. 1, Pts. 1-17.
...........1863. Enumerazione sistematica degli ofidi appartenenti al gruppo Coronellidae. Arch. Zool. Anat. Phys. 2: 213-330.
King, W. 1939. A survey of the herpetofauna of Great Smoky Mountains National Park. Amer. Midl. Natur. 21(3): 531-582.
Klauber, L.M. 1936. The California king snakes, a case of pattern dimorphism. Herpetologica 1(1): 18-27.
...........1939. A further study of pattern dimorphism in the California king snake. Bull. Zool. Soc. San Diego 15: 1-23.
...........1944. The California king snake: A further discussion. Amer. Midl. Natur. 31(1): 85-87.
...........1948. Some misapplications of the Linnaean names applied to American snakes. Copeia 1948(1): 1-14.
Küchler, A.W. 1964. Natural Vegetation. *In* Goode's World Atlas, 12th ed. Rand McNally, Chicago, Illinois: 54-55.
Lazell, J.D., Jr. and J.A. Musick. 1973. The Kingsnake, *Lampropeltis getulus sticticeps*, and the ecology of the Outer Banks of North Carolina. Copeia 1973(3): 497-503.

Linnaeus, C. 1766. Systema naturae. 12th ed. Stockholm. 532p.

Lockington, W.N. 1876. Description of a new genus and species of colubrine snake. Proc. California Acad. Sci. 7: 52-53.

Mayr, E. 1944. Remarks on Hobart Smith's analysis of the western king snakes. Amer. Midl. Natur. 31(1): 88-90.

Neill, W.T. 1963. Polychromatism in snakes. Quart. J. Florida Acad. Sci. 26(2): 194-216.

............and E.R. Allen. 1949. A new kingsnake (genus *Lampropeltis*) from Florida. Herpetologica 5(5): 101-105.

Pratt, H.B. 1923. A manual of land and fresh water vertebrates of the United States (exclusive of birds). Blakiston's Son, Philadelphia. xv + 422p.

Russell, R.J. 1964. Duration of the Quaternary and its subdivisions. Proc. Natl. Acad. Sci. 52: 790-796.

Schlegel, H. 1837. Essai sur la physionomie des serpens. Amsterdam. Sep. vol., pls. 1-21. 606p.

Schmidt, K.P. 1953. A check list of North American amphibians and reptiles. 6th ed. Amer. Soc. Ichthyol. Herpetol. viii + 280p.

Smith, H.M. 1956. Handbook of amphibians and reptiles of Kansas. 2nd ed. Misc. Publ. Univ. Kansas Mus. Nat. Hist. (9): 1-356.

............, and E.H. Taylor. 1966. Herpetology of Mexico. Reprint edition. Eric Lundburg, Ashton, Maryland.

Smith, M.A. 1928. The status of some recently described genera and species of snakes. Ann. Mag. Nat. Hist. 10(1): 494-497.

Smith, P.W. 1961. The amphibians and reptiles of Illinois. Illinois Nat. Hist. Survey Bull. 28(1): 1-298.

Soule, M., and A.J. Sloan. 1966. Biogeography and distribution of the reptiles and amphibians on islands in the Gulf of California, Mexico. Trans. San Diego Soc. Nat. Hist. 14(11): 137-156.

Stejneger, L.H. 1903. The reptiles of the Huachuca Mountains, Arizona. Proc. U.S. Nat. Mus. 25: 149-158.

...........and T. Barbour. 1917. A check list of North American amphibians and reptiles. Harvard Univ. Press, Cambridge. 125p.

Strecker, J.K. 1909. Contribution to Texan herpetology. Baylor Univ. Bull. 12(1): 1-9.

Van Denburgh, J. 1895. The herpetology of Lower California, pt. 1. Proc. California Acad. Sci., ser. 2. 5: 77-162.

...........1922. The reptiles of western North America. Occ. Papers California Acad. Sci. 10: 1-1028.

............, and J.R. Slevin. 1921. Preliminary diagnosis of new species of reptiles from islands in the Gulf of California, Mexico. Proc. California Acad. Sci., ser. 4. 11(17): 395-398.

Webb, R.G. 1961. A new kingsnake from Mexico with remarks on the Mexicana group of the genus *Lampropeltis*. Copeia 1961(3): 326-333.

............1970. Reptiles of Oklahoma. Univ. Oklahoma Press, Norman. xi + 370p.

Werner, F. 1924. Neue oder wenig bekannte Schlangen aus dem Natur-historischen Staatsmuseum in Wien. Akad. Wissenschaften Wien, Sitz. 133: 29-56.

Williams, K.L. 1970. Systematics of the colubrid snake *Lampropeltis triangulum* Lacèpède. Dissertation, Louisiana State University.

Wright, A.H., and S.C. Bishop. 1915 A biological reconnaissance of the Okefenokee Swamp in Georgia. II. Snakes. Proc. Acad. Nat. Sci. Philadelphia 67: 139-192.

............, and A.A. Wright. 1957. Handbook of snakes of the United States and Canada. Comstock, Ithaca, New York, Vol. 1. xvii + 564p.

Yarrow, H.C. 1882. Descriptions of new species of reptiles and amphibians in the United States National Museum. Proc. U.S. Nat. Mus. 5: 438-444.

Zweifel, R.G., and K.S. Norris. 1955. Contribution to the herpetology of Sonora, Mexico: descriptions of new subspecies of snakes (*Micruroides euryxanthus* and *Lampropeltis getulus*) and miscellaneous collecting notes. Amer. Midl. Natur. 54(1): 230-249.

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